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JOURNAL OF ANATOMY

ON THE SO-CALLED SYMPATHETIC CELLS IN THE SPINAL GANGLIA

By CHARLES FISHER and S. W. RANSON

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Recently F. Kiss (1932 *a*, *b*) has reported a series of experiments on the cranial and spinal ganglia of Man and different Mammals in which he used a new osmic acid staining method. The results of these experiments, if confirmed, would lead to a considerable revision of our present conceptions of the anatomy of the nervous system.

The method used by Kiss consisted of the following steps: fixation in 10 per cent. formol for 24 hours, washing in distilled water 24 hours, treatment with 1 per cent. osmic acid for from 5 to 8 days, another washing in distilled water for from 12 to 24 hours, dehydrating in alcohol series and finally embedding into celloidin-paraffin (Apathy's method). It should be noted that the essential step in this procedure is the prolonged treatment with osmic acid after a previous fixation of the ganglion in formalin. By his method of embedding Kiss believed that he had ruled out shrinkage, but his photographs show that this is not the case; further evidence in support of this contention will be presented later.

With this method Kiss was able to differentiate two types of nerve cells in the cranial and spinal ganglia of a number of Mammals. Type I is, according to him, apolar or unipolar; the cell body is pale with very fine granules and the size varies. The nucleus is uncoloured. Type II is usually small and always multipolar; the cell body is black and the granules are larger than in Type I. In human spinal ganglia he found a great majority of Type I cells, and scattered among the large pale cells single ones of Type II. But in the sympathetic ganglia of Man, monkeys and pigs Kiss was able to find only small, dark, multipolar cells (Type II). In the various cranial ganglia he found different proportions of these two types of cells, and this finding, he maintains, is confirmed by comparative anatomical studies, which show that sensory and sympathetic nerves meet in the same ganglion. These considerations led him to the conclusion that the Type I cells are sensory and the Type II cells sympathetic.

Because of the extraordinary nature of some of Kiss's results, his observations and conclusions require careful consideration before they can be accepted. For example, he found the geniculate ganglion of the facial nerve, whose sensory character is well established, to be composed exclusively of sympathetic, multipolar neurones. The same ganglion in closely related animals was found to have widely varying cellular compositions. Thus the human otic ganglion

is said to be exclusively sympathetic, while the same ganglion in the cat is largely sensory, the human geniculate to be sympathetic, that of *Cercopithecus* both sensory and sympathetic. The ciliary ganglion was found to have a large percentage, 50 per cent., of sensory cells; the spinal ganglia to have a number of sympathetic cells; the Gasserian ganglion to have about one-third sympathetic cells; the spheno-palatine ganglion of Man to have sensory cells, the superior ganglion of the glosso-pharyngeal and the jugular of the vagus a majority of sympathetic neurones; the nodose to have both types, with Type I in the majority.

It is at once obvious that these results deviate widely from the ordinarily accepted notions as to the cellular contents of these ganglia. Thus, Cajal (1911) classifies the Gasserian ganglion as the sensory ganglion of the trigeminal nerve, the geniculate as the source of the sensory fibres of the nervus intermedius of Wrisburg, the superior and petrous as the sensory ganglia of the glosso-pharyngeal, and the jugular and nodose as the sensory ganglia of the vagus. Ranson (1931) and De Castro (1932) classify the ciliary, spheno-palatine, otic and submaxillary as cranial parasympathetic ganglia.

An examination of Kiss's photographs reveals well-defined shrinkage spaces around the Type II cells. It seems possible that the black cells might be due to shrinkage, and especially so since Kiss himself noted that shrinkage influenced both the form and colour of the cells. Moreover, his preparations show not only black and light cells, but intermediate forms of all shades of grey, the darkness of the cells seemingly proportional to the amount of shrinkage present. Accordingly, it seemed profitable to repeat the work and attempt, if possible, to isolate some of the factors producing the black cells.

METHOD

The prolonged osmic acid technique was used unchanged except for the dehydration and embedding processes. Dehydration was carried out by running the ganglia through 50–70–95 per cent. absolute alcohols, then through xylol, two changes of paraffin (61–63°) and finally embedding in fresh paraffin. Serial sections were cut 7μ thick. Cats were used; they were anaesthetised with ether, then bled and killed by evisceration. The ganglia were removed as quickly as possible after laminectomy, care being taken not to traumatise them. The ganglia were all removed within 1½ hours after the death of the animal. During the excision they were kept moist with mammalian Ringer's or normal salt solutions and were transferred into formalin immediately after removal except for the following: Several spinal and sympathetic ganglia were placed in 3 per cent. salt solution for from 1 to 2 hours before fixation in formalin. Several others were crushed between forceps in order to ascertain the possible effects of trauma. As controls for the ganglia placed in hypertonic salt solution, others were treated with Ringer's solution for the same length of time. In order to compare the results obtained with fresh material with those from old material, the same cats were placed in an ice-box for 24 hours, after

which a number of spinal and sympathetic ganglia were removed and fixed in formalin.

RESULTS

The two types of cells described by Kiss were seen without any trouble, but there were also present many intermediate grey forms of all shades (fig. 1). As Kiss reports, there is a small number of black cells scattered more or less haphazard through the spinal ganglia. These black cells are almost invariably surrounded by a skrinkage space which is best developed around the darker cells (fig. 2); smaller shrinkage spaces are seen around the grey cells, but the very light cells are packed closely together and show little or no shrinkage. Not all the black cells are small as Kiss implies, although shrinkage tends to make them appear smaller than they really are. Many of the black cells have a serrated contour the depressions of which indicate the position of the satellite cells. It seems probable that the "multipolarity" of these spinal ganglion cells is an artefact produced by distortion of the cell contours through shrinkage. The effects of shrinkage are beautifully illustrated by fig. 3, which shows a spinal ganglion submitted to hypertonic salt solution. The great majority of the cells are black and many of them have the uneven contours which Kiss has mistaken for dendritic processes. The control ganglia which were placed in Ringer's solution gave the same results as the ganglia submitted to the unmodified method.

The number of black cells found in the spinal ganglia varies in different specimens. It seems likely that one of the factors producing this variation is trauma, those ganglia which suffer greater injury during excision showing a larger number of black cells. This is borne out by the results obtained with the ganglia which were purposely crushed. Fig. 4 shows a spinal ganglion treated in this way, and the great increase in black cells as compared with the ganglia subjected to the unmodified technique is obvious.

Kiss asserts that all the cells of the ganglia of the sympathetic trunks are Type II, multipolar, black cells. Our results do not confirm this. On the contrary, lumbar sympathetic ganglia treated by the unmodified technique contain only a few sporadic black cells, the great majority belonging to Type I (fig. 5). Moreover, as in the case of the spinal ganglia, treatment with 3 per cent. saline results in a very marked increase in the number of the Type II cells. According to Kiss the superior cervical sympathetic ganglion should be composed exclusively of Type II cells. We have obtained preparations in which this ganglion contained a great majority of Type I cells (fig. 6). Here again treatment with hypertonic salt solution greatly increases the number of black cells. These latter are surrounded by shrinkage spaces, as in the spinal ganglia. The light cells are oval in form, without visible processes and have no shrinkage spaces.

The results obtained from the ganglia, both spinal and sympathetic, which were left in the body for 24 hours indicate that post-mortem changes aid in the production of the black cells. Their number is greatly increased as compared with the number found in fresh material (fig. 7).

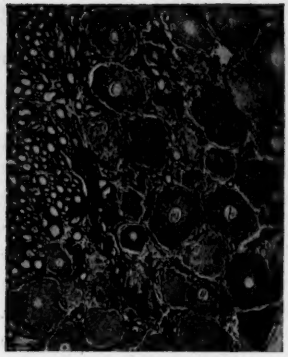

Fig. 1.

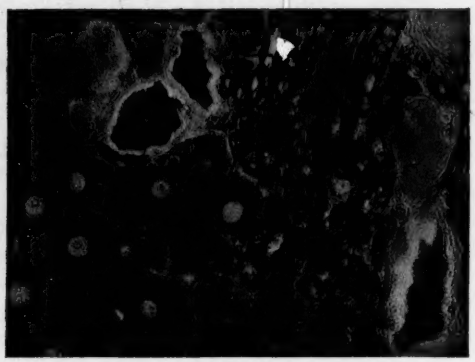

Fig. 2.

Fig. 1. From a spinal ganglion of the cat prepared by the method of Kiss. × 145. A darkly staining cell is seen in the lower right-hand corner. The other cells have taken varying shades of grey.

Fig. 2. From a spinal ganglion of the cat prepared by the method of Kiss. Three skrunken dark cells have an irregular contour. × 250.

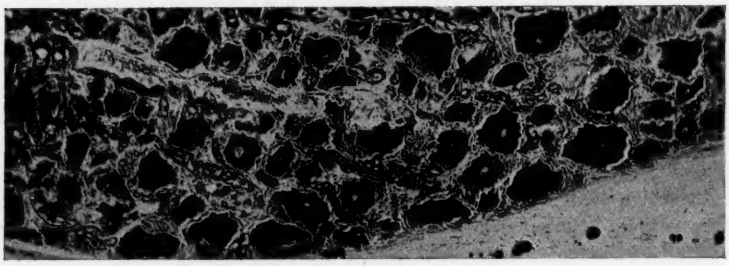

Fig. 3.

Fig. 3. From a spinal ganglion of the cat prepared by the method of Kiss. Before fixation the ganglion was treated with hypertonic salt solution. × 145.

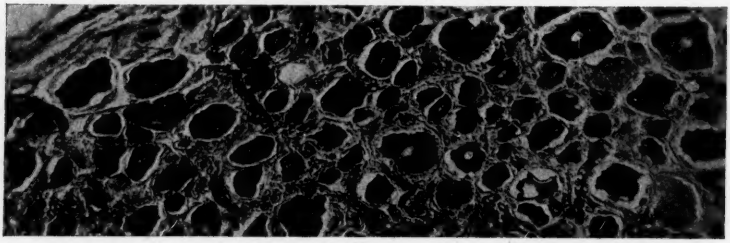

Fig. 4.

Fig. 4. From a spinal ganglion of the cat prepared by the method of Kiss. Before fixation the ganglion was crushed. × 145.

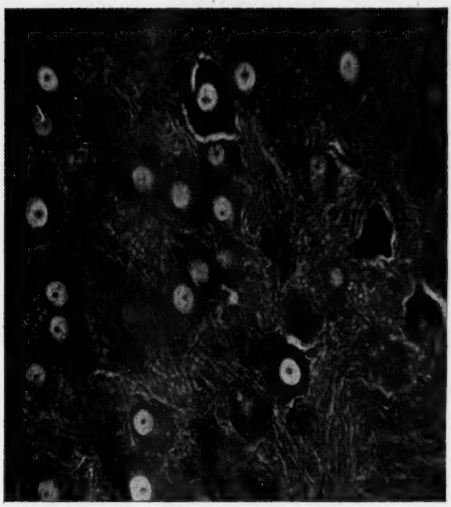

Fig. 5.

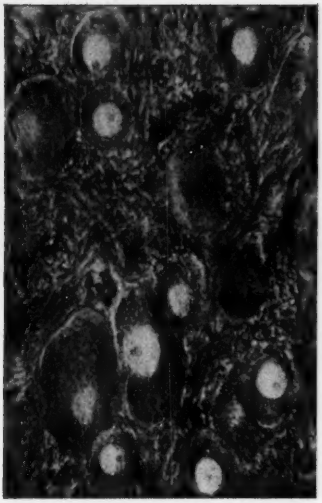

Fig. 6.

Fig. 5. From a lumbar sympathetic ganglion of the cat prepared by the method of Kiss. ×350.
Fig. 6. From the superior cervical sympathetic ganglion prepared by the method of Kiss. ×610.

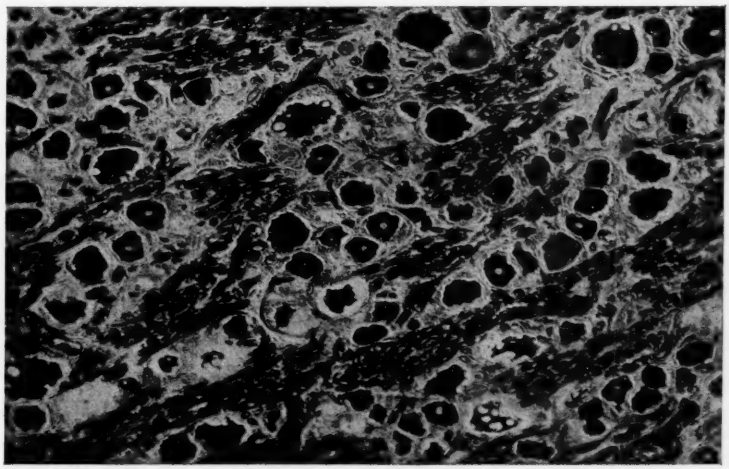

Fig. 7.

Fig. 7. From a spinal ganglion of the cat prepared by the method of Kiss. The ganglion was removed and fixed 24 hours after death. ×145.

DISCUSSION

In a recent critique of Kiss's work, G. Levi (1932) rejects the former's findings on the ground that he used an old, unsuitable technique, long since renounced by histologists in favour of the more elective methods for the staining of nerve cells and their processes (those of Golgi, Ehrlich, Cajal, Bielschowsky). He points out that an examination of Kiss's microphotographs shows that there is little staining of the fine processes of the ganglion cells, and that since the staining is incomplete, his differentiation between apolar, unipolar and multipolar cells cannot be accepted. He notes, further, that in Kiss's figures the majority of the cells are even apolar. Without presenting any experimental evidence, he suggests that shrinkage may play a part in the coloration of the cells and concludes that neither the light or dark staining, the form and distribution of the cell granules, nor the different cell sizes have value as differentiating characteristics between the sensory and sympathetic ganglion cells. The experimental evidence presented above confirms in every way Levi's opinion that the prolonged osmic acid treatment is completely unsuitable for the purpose to which Kiss has applied it.

Kiss's evidence for the sympathetic character of the Type II cells is largely presumptive. Because he found all the cells of the ganglia of the sympathetic trunks to have the characteristics of Type II, he concluded that those cells which stain black with the prolonged osmic acid method elsewhere in the nervous system are also sympathetic in function. Since evidence has been presented above which indicates that the sympathetic ganglia are composed almost exclusively of Type I cells, the few Type II cells present most probably being shrinkage products, this line of reasoning is invalidated. Furthermore, our results show that the black cells can be produced experimentally by treating the ganglia with hypertonic salt solution, and that post-mortem changes and injury to the ganglia cause an increase in their number.

The number of black cells in the different ganglia varies from case to case; sometimes a spinal ganglion will have very few and at other times a comparatively large number of these dark forms. This is not surprising, however, if we consider that a number of factors seem to influence their production, e.g. shrinkage, post-mortem changes, trauma.

It seems probable that Kiss found these black cells so frequently and in such diverse ganglia, sensory as well as sympathetic, because he used old, injured or shrunken material. In this connection it should be noted that Bacsich (1932), one of Kiss's colleagues, asserts that one of the virtues of the prolonged osmic acid method is its applicability to post-mortem material, 12–24 hours old.

Whatever the Type II cells represent, products of a purely physical or mechanical process or of a chemical reaction, it seems certain that they do not indicate a greater lipoid content of the sympathetic cells as opposed to the sensory, as Bacsich (1932) maintained.

Much of the evidence from the literature which Kiss cites in support of his contention that there are sympathetic cells in the spinal and various cranial ganglia, and also sensory cells in ganglia usually considered as sympathetic, can be interpreted with better logic against him. In support of the view that there are multipolar cells in the spinal ganglia he cites some of the older work of Dogiel, Lenhossek, Spirlas and also Cajal (1906). However, this latter author has recently (1928) repudiated his earlier opinion, for he states in his discussion of spinal ganglion cells: "The monopolar ganglionic type is the most abundant and frequently the only one found. For that reason we consider it to-day as the normal neurone, that is, a neurone exempt from the phenomena of decadence and regeneration. From time to time, however, one sees, especially in the adult and the old, other cellular types." Further on he declares, "We all supposed that, besides the classical monopolar type of cell, the sensory ganglia contained a few multipolar neurones and certain nerve nests, which were considered as the terminal apparatus either of exogenous fibres (Cajal) or of ramified axons belonging to autochthonic neurones (Dogiel). But later investigations imposed a change of opinion. To-day it seems indubitable that these multipolar cellular types, as well as the pericellular nests, represent structures of a pathological and more or less ephemeral character."

De Castro (1921, 1932) points out that the great majority of the cells of the spinal and sensory cranial ganglia are unipolar. There are a few atypical cells in normal human ganglia, which the Spanish school has studied intensively. These atypical multipolar forms are considered to be sensory cells, not sympathetic, which increase in old age and various pathological conditions. De Castro reports, for example, 1–4 per cent. fenestrated cells in the nodose and jugular of the vagus of the infant and normal adult; apart from these there may be a few cells with terminal bulbs and a few ragged or erethised types. It should be noted that Kiss finds the jugular ganglion to contain a great majority of sympathetic cells.

From Kiss's figure of the Gasserian ganglion of Man at least one-third of the cells appear to be Type II. He cites Takeda (1924) in support of this finding. This latter author studied the Gasserian ganglion of the ox, using the Cajal method. He found in fifty microscopic fields 2801 unipolar, 55 bipolar and only 12 multipolar cells, this last figure representing less than 0·5 per cent. of the total. An examination of Takeda's illustrations shows that these multipolar cells are the atypical sensory cells described by Cajal and De Castro, and cannot be considered sympathetic cells as Kiss maintains. Among them can be seen a fenestrated type, several cells similar to those whose axons arise by multiple rootlets and one with terminal end-bulbs.

Recently Barris and Ranson (1933) found only a small fraction of 1 per cent. of atypical cells in the spinal ganglion of the cat; all the rest of the cells were unipolar. They also showed that these cells increase in number if the ganglia are injured, the increase being a reaction to noxious influences. This agrees with Cajal's statement that these forms are pathological manifestations,

representing an attempt on the part of injured cells to regain their functional integrity.

Kiss's figures reveal a good many Type II cells in the nodose ganglion of Man, *Cercopithecus* and the pig. In a recent paper Ranson, Foley and Alpert (1933) report that, in addition to fenestrated cells, only two apparently multipolar cells could be found in half of a nodose ganglion; these could be interpreted as cells whose axons had several long roots. They saw no cells with long dendrites, like those seen in sympathetic ganglia, in the two nodose ganglia examined. More important evidence against the theory, supported by Kiss (1932 *c*), that the nodose ganglion contains synapses between the pre- and post-ganglionic parasympathetic neurones, is the fact that Ranson, Foley and Alpert were unable to find a trace of the intercellular plexus of fine branching pre-ganglionic fibres which forms such a characteristic feature of sympathetic ganglia.

According to Kiss the unmyelinated fibres in the spinal nerves are the post-ganglionic axons whose cells of origin are the Type II cells of the spinal ganglia. There is a discrepancy here, for Kiss found only a small number of Type II cells in the spinal ganglia, not nearly enough to account for the large number of unmyelinated fibres which Ranson and Davenport (1931) have shown to be present in the cutaneous nerves. Dogiel (1908) and Cajal (1906) showed that the small cells of the spinal ganglia give rise to unmyelinated fibres which divide, just as do the myelinated fibres coming from the large cells, into a branch that is directed peripherad into the spinal nerve and a finer branch that is directed centrad into the dorsal root. Later Ranson (1912) confirmed this. Previously he had made the important observation (1911) that these small cells and their unmyelinated axons are very numerous, making up 70 per cent. of the total number of cells.

Further, Kiss considers the "spinal parasympathetic nerves" of Ken Kuré (1928–31) to be the pre-ganglionic fibres which synapse with the Type II cells in the spinal ganglia. Other workers have been unable to confirm Ken Kuré's findings. Thus, the small fibres which he found in the central stump of the dorsal root after cutting the latter proximal to the ganglion, Tower (1931) found to be regenerating fibres growing into the dorsal root from the injured ventral root. Also Hinsey's (1933 *a*, *b*, *c*) careful work shows that Ken Kuré cannot possibly be right.

In support of his assertion that the spheno-palatine ganglion is both sympathetic and sensory Kiss refers to the work of Stewart and Lambert (1930) on this ganglion. He states that these authors found pain or circulatory and secretory troubles of the nasal cavity to be dependent upon the spheno-palatine ganglion, and that anaesthesia or extirpation of this ganglion helped in many cases. Reference to the work of Stewart and Lambert shows that these authors are flatly opposed to the view that the spheno-palatine ganglion is concerned with this type of neuralgic pain. They state "That the spheno-palatine ganglion, though closely associated with the sensory nerves, is a part of

the efferent nervous system cannot be too strongly emphasised." Further, they declare, "The explanation of the pain, as pointed out by Cushing, is that any pathological lesion which may set up irritation in the spheno-palatine ganglion is just as likely to irritate the main trunk of the superior maxillary nerve or its branches."

Finally, it should be noted that Kiss finds half of the cells of the human ciliary ganglion to belong to Type I. This ganglion is usually conceived of as purely parasympathetic. Thus, Marinesco, Parhon and Goldstein (1908) and Müller and Dahl (1910), who studied the ciliary ganglion intensively in Man and different Mammals, found only multipolar ganglion cells; both of these investigations were carried out with silver stains. In a recent exhaustive study, Pines (1927) found the great majority of the cells of the ciliary ganglion to be multipolar, but he did note a few bipolar and unipolar cells. These were confined to the periphery of the ganglion, while Kiss's sensory cells are scattered throughout. It is very improbable that these latter are the same cells found by Pines.

CONCLUSIONS

After fixation in formalin, prolonged treatment with osmic acid causes a small proportion of the cells in the spinal and sympathetic ganglia to become black, while others are lightly stained and still others take various shades of grey. The depth of the stain seems to be related to the amount of shrinkage.

If before fixation the ganglion is treated with hypertonic salt solution, or is crushed, the number of the shrunken dark cells is increased. Delay in fixation, allowing post-mortem changes to occur in the ganglion, also increases the number of dark shrunken cells.

No evidence has been found in support of the theory, proposed by Kiss, that the dark cells in the spinal ganglia are sympathetic.

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THE DEVELOPMENT OF THE HYPOPHYSIO-PORTAL SYSTEM IN MAN

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In recent papers Popa and Fielding(1,2) have described in the human subject a system of vessels running in the stalk of the pituitary which they call the hypophysio-portal veins. The development of this system is the subject of this paper.

MATERIAL AND METHOD

I have had the advantage of being able to study two early embryos, one of 11·9 mm. and the other not measured but probably about 5 weeks from conception, placed at my disposal at Oxford by Prof. Goodrich, for whose kindness in allowing me to examine and photograph them I am most grateful. I have also made use of three later specimens of about 2, 4, and 5 months, generously given to me by medical practitioners. These pituitaries were sectioned at 10 μ together with all the surrounding structures after fixation in mercury formol soon after death. The sections were stained with Mallory's connective tissue stain, modified for certain sections to show particular points. The series were then examined, the courses of the chief vessels determined, and the most important sections were photographed.

OBSERVATIONS

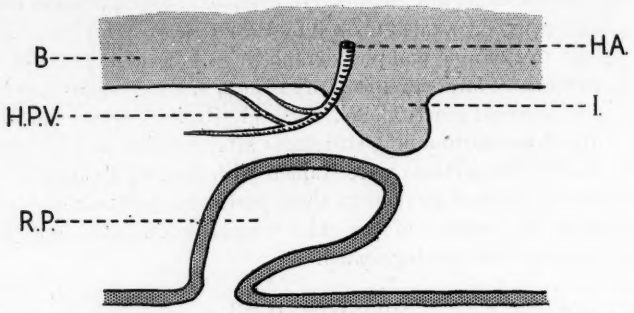
Plate I, fig. 1, shows a transverse section of an 11·9 mm. embryo at the region in which the carotid arteries are bent to conform with the flexure of the embryo. The arteries therefore lie in the plane of the section. The mesoderm immediately surrounding the brain, richly supplied with blood vessels, is about to form the meninges. Vessels are carried into the substance of the brain by this tissue growing in. When, later on, the different membranes can be distinguished, the vessels can be seen to be accompanied into the brain by pia mater and by arachnoid tissue. Each vessel comes in this way to be surrounded by a small diverticulum of the sub-arachnoid space—the space of Virchow-Robin.

According to the observations of Hughson(3,4) upon the adult dog and cat and the embryo pig, the pituitary complex in these forms lies wholly within the dura mater which covers the floor of the sella and is reflected to form the diaphragma sellae. The cord of cells from the buccal epithelium marking the closed tube of the original buccal invagination (Rathke's pocket) breaks down before the completion of the meninges, so that this total enclosure of the complex is developmentally comprehensible. The arachnoid membrane also encloses the complete organ. There is inside this and separated from it by a part of the sub-arachnoid space, a layer of pia mater. Hughson demonstrated

this by injecting a medium into the sub-arachnoid space of his subject and observing that it appeared all round the pituitary and that it entered the pars anterior round the vessels leading to and from it. That is to say it was forced into the buccal analogues of the spaces of Virchow-Robin.

This description of the relations of the parts differs from the account by Parker (5) of the condition in *Trichosurus* and *Perameles*. Here, while the whole complex lies within the dura mater, the pars nervosa and the isolated pars tuberalis are alone within the pia mater.

Since the parts of the pituitary complex appear when the brain is surrounded by undifferentiated tissue, the nervous portion pushes down into formless mesoderm and the buccal portion pushes up into the same substance. The mesoderm which is trapped between the pars nervosa and the pars intermedia, bearing blood vessels, may, if it seems desirable, be termed pia mater, but since the membranes are formed as such out of undifferentiated mesoderm after the



Text-fig. 1. A diagrammatic representation of the relations of the hypophysial artery, the infundibulum, Rathke's pocket, and the brain.

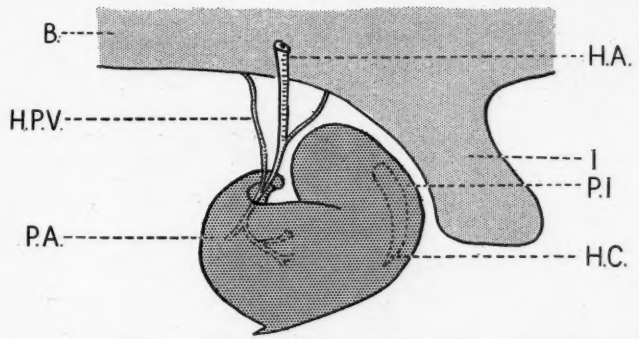
pituitary complex is established it is not surprising that difficulties are experienced and apparent anomalies found in efforts to trace their actual continuity.

A branch of a vessel supplying the brain can be seen invading it at ***S.A.B.*** in Plate I, fig. 1. Actual invasion of the substance of the brain is less advanced ventrally than laterally, though ventrally the closely applied mesoderm is very vascular. At ***H.A.*** in the same figure a conspicuous branch is seen springing from the carotid and running medially and forward in this connective tissue between the developing hypophysis and the brain. The same thing can be seen on the other side. These relations are indicated diagrammatically in text-fig. 1. The same vessels are seen again in Plate I, figs. 2–4. These sections are taken further forward where branches (***H.P.V.***) run from the vessels to the ventral surface of the brain. There is thus an arterial link from this tissue to the brain established even at this early stage.

The great venous sinuses beneath the brain surround the developing pituitary, and some connection is maintained between them and the vascular

system of the organ, the connections penetrating the capsule when this is formed through actual discontinuities in it. These connections remain small at the ages which are here considered, and the definite hypophysial veins described by Popa and Fielding cannot be demonstrated in my material. It has proved impossible also to confirm the suggestion of Brander (6) that the hypophysial cleft becomes confluent with the venous system. The vessel which he describes as running back from the point where the buccal cord enters the sella to the ventral end of the cavity of the pituitary can be clearly seen in the later stages but remains outside the capsule. Venous spaces are beginning to appear in the mesoderm beneath the brain at the stage shown in Plate I, fig. 1, and at ***H.V.*** one can be seen entering the head vein.

Plate II, fig. 5, shows a later stage, in which the invasion of the brain by vessels is further advanced laterally (***S.A.B.***), though still slight ventrally. The artery previously described as running forward between the brain and the

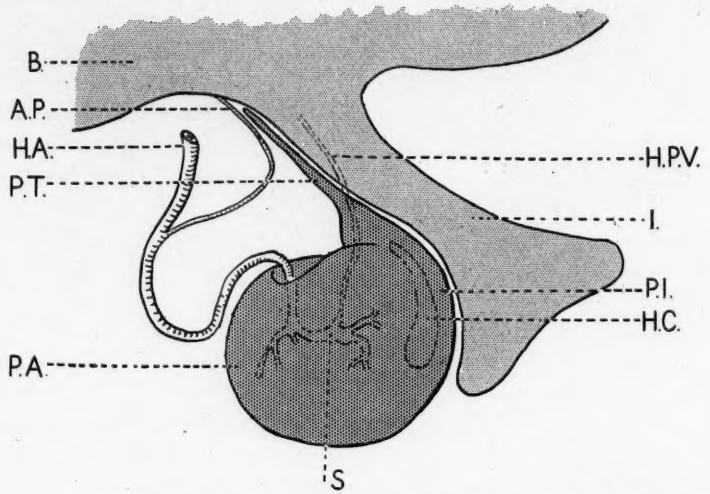


Text-fig. 2. A diagrammatic representation of the relations of the hypophysial artery, the infundibulum, the pars anterior, and the brain. The pars anterior is lapping round the hypophysial artery and its branches to the brain. The left side only is shown.

pituitary can be clearly seen leaving the carotid, and can now be identified with the hypophysial artery (***H.A.***). The connective tissue in which it runs is by now becoming surrounded by the upgrowing lateral horns of the pars anterior, as can be seen in Plate II, fig. 6 (***C.T.***), and as is indicated diagrammatically in text-fig. 2. This growth leads to the conspicuous core of connective tissue seen in ordinary transverse sections of the human pituitary, and is thus seen to be part of the layer of connective tissue which forms the pia mater elsewhere all round the central nervous system. This core comes on each side to be almost completely built in by glandular tissue, but it remains in continuity with the rest of the connective tissue of the region at one point, and it is here that the hypophysial artery enters the pituitary (see text-figs. 2 and 3 and Plate II, figs. 7 and 8).

Within this core of connective tissue the artery, which may be single or double, or reduced or absent on one side, enlarges to form the sinusoids com-

monly described and seen in Plate III, fig. 9, at *S*. These sinusoids are large thin-walled vessels with an endothelium probably complete, though extremely attenuated. They ramify and anastomose in all directions, bringing the blood into the most intimate contact with the outer side of the acini of the glandular portions of the pituitary. The secretory cells are arranged so that the basiphil elements are towards the connective tissue and vessels, while the acidophil elements are towards the acini—unlike the condition found by de Beer in *Scyllium* (7). There is a very intensely acidophil area in the pars intermedia whose cells line the cleft. The cavities of the acini are derived from the original hypophysial cleft by a process of folding and the nipping off of evaginated portions.

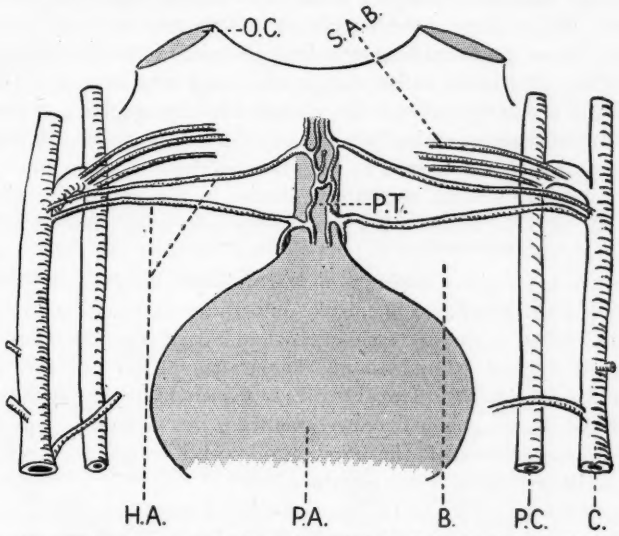


Text-fig. 3. A diagrammatic representation of the relations of the hypophysial artery, the infundibulum, the pars anterior, the pars tuberalis, and the brain.

Part of the blood which reaches the pituitary by the hypophysial artery makes its way back into the general circulation by way of the venous connections previously described, but part of it must, it seems, be carried on from the earliest stages here studied by the vessels seen in Plate I, figs. 3 and 4, to a site beneath the brain. The heavy invasion of the ventral portion of the brain in this region is accomplished by branches of the pituitary vascular system. Such a branch is seen in Plate III, fig. 12. This is a hypophysio-portal vessel.

Further evidence about the nature of the portal vessels of the pituitary can be obtained from a study of the manner in which the vascular system of the pars tuberalis develops. The pars tuberalis pushes up the rostral aspect of the stalk, closely applied to the brain, and between the nervous tissue and the pia mater. This may be seen in Plate III, figs. 10 and 11. In doing so it interferes

with a part of the arterial supply of this region of the brain, which is provided by invading twigs from a network confluent with the carotids and comparable with the network described by David (8) in other forms. In Plate III, fig. 10, this network is cut several times, and at *A.P.* an artery of the pia mater is seen actually in process of being involved in this upgrowing glandular tissue. These relations are indicated diagrammatically in text-fig. 3, and a reconstruction of this network in one embryo is shown in ventral view in text-fig. 4. In Plate III, fig. 11, a vessel from the sinusoids of the pars tuberalis is seen invading the brain. While the vessel seen in Plate III, fig. 10, does not invade the brain as a whole, its branches do, and it seems that these two vessels are to be inter-



Text-fig. 4. A squared-paper reconstruction of the relations of the arteries, the pituitary, and the brain in one embryo of 4½ months. Seen from the ventral side.

preted as showing two stages in the establishment of a part of the hypophysio-portal system. The colloid described by Popa and Fielding in these vessels has not been found in my material. Possibly it does not appear till later.

DISCUSSION

It is suggested that the hypophysio-portal vessels are morphologically branches of the carotid destined originally to supply the brain and quite secondarily involved in the pituitary complex simply because of the proximity of the pituitary to their path. On this view they are comparable to any other vessels bringing blood to the brain, and are really arterial in origin. They become sinusoid on being appropriated by the pituitary, but regain something of their original form when they reach their proper destination—the brain. In

the tissue of the floor of the brain they break up into capillaries just as any other supplying vessels might. From these capillaries—the secondary distribution net of Popa and Fielding—the blood is removed by the ordinary systemic veins of this part of the brain.

The vessels have been termed by Popa and Fielding the hypophysio-portal *veins*, indicating their function of removing blood and secretions from the pituitary. While it is obviously very difficult to distinguish usefully between veins and arteries in this region, since both may be thin-walled and since anastomosis is so free that some reversal of flow may well occur, yet it is not easy to see why, if these vessels are to be regarded as veins, and a vein is taken to be a vessel normally conveying blood towards the heart, they should run to the brain. The analogy of the hepatic-portal vein does not help to make this clear, since, there, a pre-existing vein is appropriated by a developing gland and continues afterwards on its way to the heart as a vein still. Here the topography of the parts makes it almost impossible to imagine a vein from the pituitary to the heart becoming involved in the brain. Even if such a pituitary vein were so involved it is hard to see what developmental factors would be likely to cause it to break up into capillaries in the brain. The violent rearrangement of tissue which takes place in the liver hardly has an analogy in the brain.

If the vessels are veins coming from the brain and involved on their way in the pituitary, then their function must be quite different from that envisaged by Popa and Fielding, unless a reversal of flow and indeed of function has occurred to an extent difficult to understand. These authors have described colloid which has been thought to travel up these vessels from the pituitary to the brain. Moreover, the venous connections from the pituitary seem quite inadequate in my material if the hypophysio-portal vessels are considered as bringing additional blood to the pituitary.

These difficulties seem to be lessened if the hypophysio-portal vessels are regarded as part of the arterial supply of the brain. While the concept of a portal artery is not commonly employed, yet it may be argued that the carotid artery of the frog is nothing less. Here blood is conveyed from the capillary system of the carotid gland to the capillaries of the head. In the fish the whole arterial system is broken down in the gills and re-collected by the efferent arteries. In the eel, Woodland (9) has described an artery to the air bladder breaking up into the rete mirabile, the strands of which are re-collected, to break up into capillaries further on their course.

Concerning the ways in which this system could effectively transport material from the pituitary to the brain, the interesting suggestion of David (8) may be noted: that the pulse of the adjacent carotids might be communicated to the pituitary so as rhythmically to expel its contents.

While Hughson (3, 4) has shown that the vessels entering the pars anterior are accompanied by these spaces of Virchow-Robin, it has been held by Basir (10) that in the dog the hypophysio-portal vessels are not so accompanied, though

the systemic vessels in the brain are. While it is extremely difficult to be sure of a point of this kind from microscopical examination without injection, it may perhaps be added that I have not been able to recognise arachnoid tissue round these vessels in my material. It seems probable that vessels growing from the pars anterior to the brain would not carry with them any recognisable arachnoid tissue, since, on the view I have suggested, they could be regarded as starting from the pia mater.

CONCLUSIONS

1. The hypophysio-portal vessels are a part of the arterial supply of the brain.

2. This part of the arterial supply has been secondarily involved and enclosed by the upgrowing wings of the buccal part of the pituitary when it was close to the under-surface of the brain.

3. As the infundibular stalk lengthens, the vessels assume their distinctive form.

I wish to thank Prof. A. C. Hardy, in whose Department most of the work was done, for his encouragement, and Dr G. R. de Beer for reading the paper in typescript and making many helpful suggestions.

EXPLANATION OF LETTERING

A.	Acini.	*III.*	Third ventricle.
A.P.	Artery of pia mater.	*O.C.*	Optic chiasma.
B.	Brain.	*P.A.*	Pars anterior.
C.	Carotid.	*P.C.*	Posterior communicating artery.
C.T.	Connective tissue core of pars anterior.	*P.I.*	Pars intermedia.
		P.M.	Pia mater.
H.A.	Hypophysial artery.	*P.T.*	Pars tuberalis.
H.C.	Hypophysial cleft.	*R.P.*	Rathke's pocket.
H.P.V.	Hypophysio-portal vessel.	*S.*	Sinusoid.
H.V.	Head vein.	*S.A.*	Sub-arachnoid space.
I.	Infundibulum.	*S.A.B.*	Systemic artery of brain.

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EXPLANATION OF PLATES

Plate I.

Fig. 1. Transverse section through the pituitary of an 11·9 mm. embryo, showing the origin of the hypophysial artery from the carotid on each side. ×48.

Fig. 2. Same as fig. 1, but further forward, showing course of hypophysial artery. ×48.

Fig. 3. Same as figs. 1 and 2, but further forward, showing connection between hypophysial artery and brain. ×48.

Fig. 4. Same as figs. 1, 2 and 3, but still further forward, showing a similar connection on the other side. ×48.

Plate II.

Fig. 5. Transverse section through the pituitary of a later embryo, showing the origin of the hypophysial artery from the carotid on each side. ×30.

Fig. 6. Same as fig. 5, but further forward, showing enclosure of core of connective tissue with vessels by the upgrowing lateral lobes of the pars anterior. ×30.

Fig. 7. Para-median section of a 4-months' embryo, showing hypophysial artery approaching the pituitary. ×28.

Fig. 8. Similar to fig. 7, but showing the hypophysial artery cut twice, once inside and once outside the pituitary. ×28.

Plate III.

Fig. 9. An enlarged view of part of the connective tissue core, showing sinusoids and acini. ×130.

Fig. 10. Para-median section of the pituitary of a 4-months' embryo, showing artery of the pia involved by developing pars tuberalis. ×28.

Fig. 11. Para-median section of the pituitary of a 4-months' embryo, showing a hypophysio-portal vessel from the pars tuberalis entering the brain. ×28.

Fig. 12. Para-median section of the pituitary of a 4-months' embryo, showing a hypophysio-portal vessel well established, with thick glial sheath. ×28.

Fig. 2.

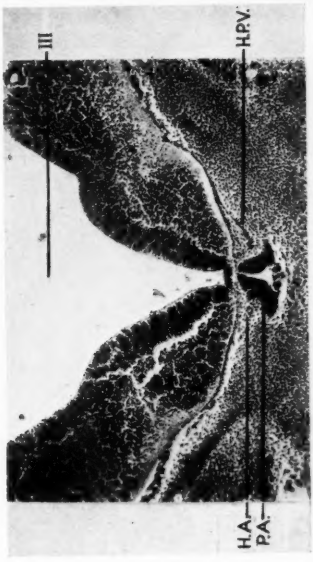

Fig. 4.

Fig. 1.

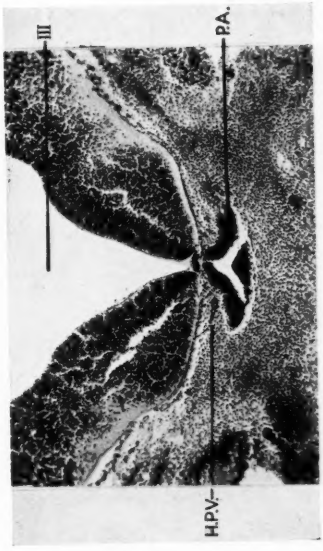

Fig. 3.

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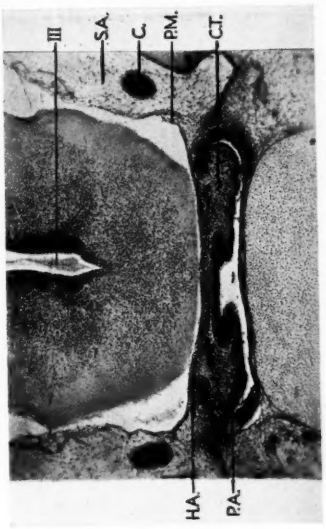

Fig. 6.

Fig. 8.

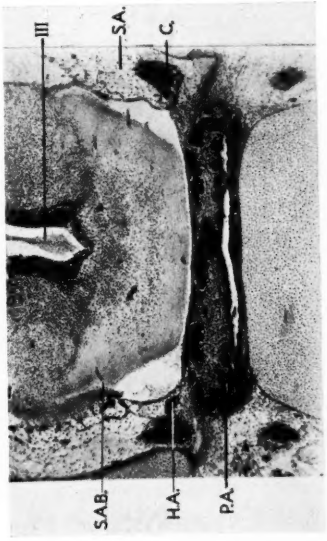

Fig. 5.

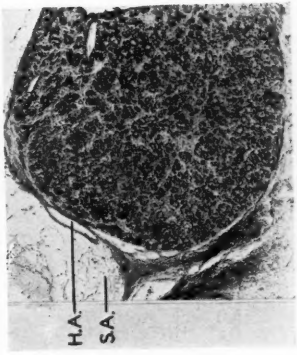

Fig. 7.

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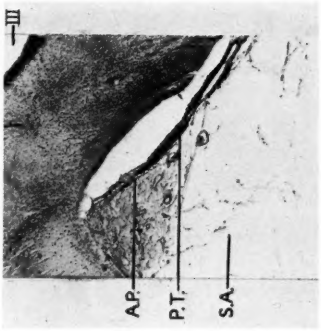

Fig. 10.

Fig. 12.

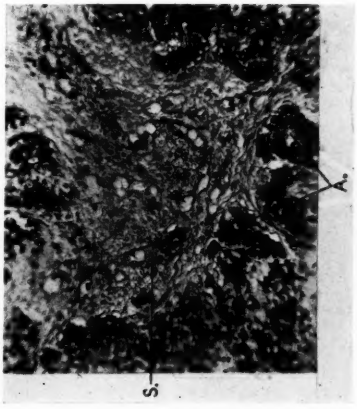

Fig. 9.

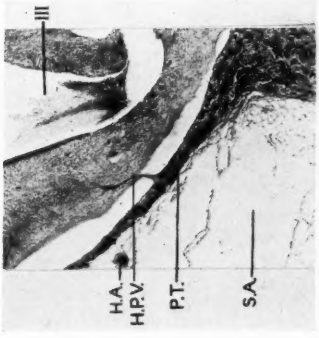

Fig. 11.

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THE SUPRARENAL CORTEX IN MONKEYS OF THE GENUS *PITHECUS*

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I. INTRODUCTION

The history of the human suprarenal gland, from the time of appearance of its earliest primordia up to the important changes occurring during the first two years of post-natal life, is now fairly well known (*vide* the papers of E. E. Glynn (1912), and of M. F. Lucas Keene and E. E. Hewer (1927)). The present state of knowledge on the growth of the gland during the period immediately succeeding birth is admirably summed up by W. Cramer (1928), who, incidentally, gives the best figures of the various stages of the gland that have yet been published. The main changes taking place during this important period of the suprarenal's history concern the fate of that large part of the gland known as the "foetal cortex" or "boundary zone." This forms the greater part of the gland during foetal life and during the first few months succeeding birth. It occupies the centre of the gland, and on this account Cramer has termed it the "central body." Its periphery is enclosed in a thin rim of "true cortex," whilst in the middle the medulla is represented by a few scattered islets of chromaffin tissue only. Elliot and Armour (1911), who were the earliest to point out the existence of this "foetal cortex" in the English literature on the subject, made the error of restricting its presence to the human gland. Lucas Keene and Hewer (*loc. cit.*) made the suggestion that Comparative Anatomy might throw some light on the significance of the structure. Acting on this suggestion the present writer (1930) described the "foetal cortex" in lower Primates, in which it was found to occur in the new-born in much the same condition as in Man. As regards lower Mammals, a considerable amount of work still needs to be done before satisfactory conclusions can be drawn. The present paper is intended to give an account of the history of the cortical changes occurring in the suprarenal gland during the life history of the monkeys of the genus *Pithecus* (formerly *Semnopithecus* and *Presbytis*). The description of the suprarenal cortex in subhuman Primates was, in the writer's former contribution, based on isolated specimens of Macaques, and on two young Lemuroid suprarenals. The present account is based on specimens all belonging to the same genus, representing different age and sex factors. It is hoped to follow up this account by similar ones on the suprarenal in *Macaca sinica* and in the primitive Lemuroid, *Loris tardigradus*.

II. MATERIAL AND METHODS

The monkeys used for this work form a series representing progressive stages in the life story of the animal. They belong to the two Ceylonese species of the genus *Pithecus*, namely *P. senex* (purple-faced langur) and *P. entellus thersites* (Ceylonese race of Madras langur). Two foetal stages are described, followed by stages representing different life periods after birth. Two specimens are described from pregnant females, for pregnancy appears to have an important effect on the gland. Another factor that may have a very important effect on the suprarenal is that of climate. Climate has tremendous effects on the form and colour of the different geographical races of *P. senex*, no less than five of which have been described by different observers; and it is possible that these differences are due to climatic effects on the endocrine glands, especially the suprarenal and thyroid. Cramer (*loc. cit.*) has dealt with this subject fully for *Homo*, but the material at present available for application of the same theory to the *Pithecus* monkeys is wholly inadequate. It is hoped to investigate this problem when more material is available from the different climatic zones in Ceylon.

In all cases the suprarenals of the specimens examined have been accurately measured, and the measurements compared with those of the corresponding kidneys. The latter form a useful indication of bodily proportions, but not an absolutely reliable one. Therefore, in the case of the post-natal animals, the body weight has been recorded also wherever possible.

In sectioning the glands fresh sections have been examined in most specimens, for the different cortical zones can generally be distinguished from their characteristic colours, as pointed out in the former contribution. It must be borne in mind in this connection that in the case of the suprarenals of foetal Primates the main mass of the gland consists of cortical tissue, and the pale tissue in the middle of the gland must not be mistaken for medulla as has frequently been done. One still finds an old diagram of Allen Thomson's of a human foetal suprarenal with the foetal cortex labelled as medulla (as in vol. II, pt. 2 of the 11th ed. of Quain's *Anatomy*, p. 328). The medulla, of course, at this stage is not a macroscopic entity at all.

For microscopic study suprarenals of all the monkeys examined were fixed in equal parts Muller's fluid and 4 per cent. formalin. Sections were generally cut in the sagittal plane so as to get comparable results in all cases. The sections were made by the freezing microtome and also by the paraffin method. The frozen sections were stained with Sudan III and counterstained with haematoxylin. The paraffin sections were stained with haematoxylin and eosin. Drawings of the sections were made by marking off the limits of the different zones with the aid of a camera lucida. The details were filled in afterwards freehand, with the sections under observation during this procedure.

MEASUREMENTS

The following table gives a complete list of the measurements, in millimetres, of the kidneys and suprarenals of all the monkeys examined, together with details regarding age, race and sex.

			Suprarenals						Kidneys					
			Left			Right			Left			Right		
	Description of animals	Sex	Ht.	Br.	Th.	Ht.	Br.	Th.	L.	Br.	Th.	L.	Br.	Th.
(1)	*Pithecus senex vetulus* foetus, 72 mm. C.R.	♂	5·5	6·0	3·5	7·0	5·5	3·5	9	5	4	8·5	6	4
(2)	*P. s. vetulus* foetus, 96 mm. C.R.	♂	7·0	8·0	3·0	8·0	9·0	4·0	14	9	5	13	8	5
(3)	*P. s. nestor*, ½ grown, 232 mm. C.R.	♀	15	10	6	15	11	6	27	16	10	27	17	10
(4)	*P. s. vetulus*, ½ grown, 283 mm. C.R.	♂	13	8	5	17	10	6	27	16	10	27	17	12
(5)	*P. s. nestor* immature, 379 mm. C.R.	♀	11	10·5	3	10	8	3	21	14	10	27	13	6
(6)	*P. s. vetulus* adult	♂	14	14	4	15	8	5	46	26	17	40	25	15
(7)	*P. s. vetulus* adult, non-pregnant	♀	16	11	6	15·5	11	5	43	28	15	42	28	16
(8)	*P. s. vetulus* adult, pregnant (advanced)	♀	23	16	7	27	17	8	50	30	20	50	30	18
(9)	*P. entellus thersites*, 3–4 months old, 275 C.R.	♂	15	12	6	15	12	5·5	27	15	13	27	16	11·5
(10)	*P. e. thersites* adult, early pregnancy	♀	23	18	8	38	13	7	57	34	23	57	35	20
(11)	*P. e. thersites* adult, aged	♂	21	14	2·5	—	—	—	57	32	21·5	—	—	—

III. DESCRIPTION OF THE SUPRARENALS OF *PITHECUS SENEX*

(1) *Foetal specimens*

Two foetal specimens of *Pithecus senex* have been examined. Both belonged to the race from the wet south-western lowland area of Ceylon, *P. s. vetulus*. The older specimen was removed from a female which died in captivity. It measured 96 mm. sitting height, and corresponded to a human foetus of about the 6th month of intra-uterine life. The other was taken from a female shot in the jungle, the foetus being dissected and its suprarenals fixed, for further study, on the spot. This specimen was in an earlier stage of development, the foetus measuring only 72 mm. sitting height, and thus corresponding to a 4th or 5th month human foetus.

The measurements of the suprarenals are given in the foregoing table, whilst the general appearance of the kidneys and suprarenals can be made out from fig. 1, where the older specimen is figured at A.

From fig. 1 it can be seen that the suprarenal of the foetal *Pithecus* monkey has the same general shape and the same relative size, compared with the corresponding kidney, as in the human foetus and the foetal Macaque. In the younger specimen the suprarenal is almost as large as the corresponding kidney. In the older foetus the kidney has grown relatively more than the suprarenal, and has become lobulated on the surface. The growth of the gland has been greater in its lateral extent than in its cranio-caudal measurement. In thickness the two glands are about equal. The older suprarenal has a more conical apex than the younger one, which is more rounded. Apart from the presence of a deep fissure on the anterior face of the gland, the surface is in

both specimens quite smooth. The fissure referred to is for the exit of the large suprarenal vein. In section the gland in both foetuses is solid, and the outline smooth and uniform. It is not trifoliate. The thickest part is at the base, where the organ rests on the kidney. The latter makes a shallow concavity on the base of the suprarenal in each case. The superficial part of the gland, as seen on the sectioned surface, presents an almost homogeneous character extending nearly to the centre of the gland. It is pale pink in colour. At the centre can be seen the central vein making its way forwards

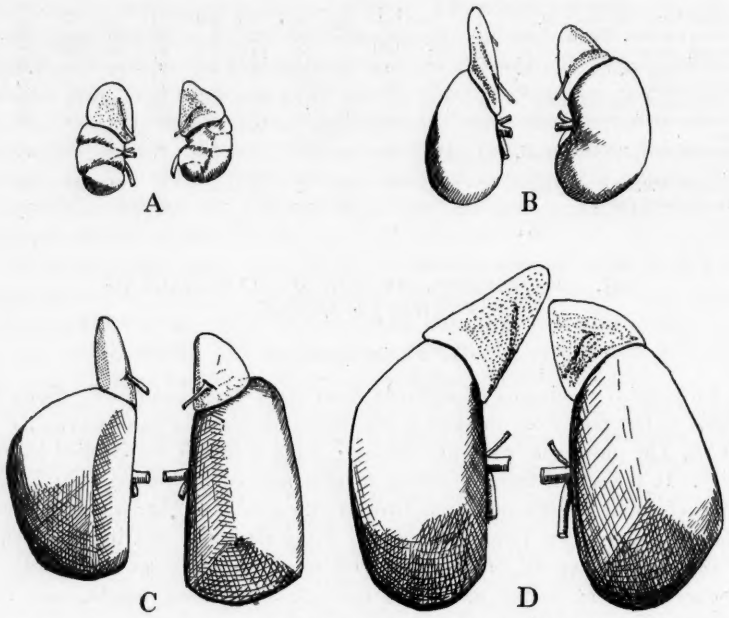

Fig. 1. Drawings of the suprarenals and kidneys of a series of purple-faced monkeys (*Pithecus senex*). All drawn to the same scale. A. Anterior view of the suprarenals and kidneys of a foetal male *P. s. vetulus*, 96 mm. C.R. length. B. Same of young male (half-grown) of the same race. C. Same of an adult male. D. Same of a pregnant female.

to leave the gland just below the middle of the ventral surface, by passing through the deep and superficial zones. Around the vessel can be seen a darker, more vascular tissue. At the ventral surface this is not distinctly marked off from the pink peripheral tissue, but on the dorsal side the separation is more distinct. In the suprarenal of the older foetus there is much more distinct zonation on the surface of the section. The main mass of the gland is made up of "foetal cortex." This presents the characteristic striated appearance due to the engorgement of the fine radially running vessels between its constituent cell columns. Around the periphery of this is the superficial

cortex consisting of a rim of pale cream-coloured, firm tissue. This older gland corresponds closely with the description given of the suprarenal of the foetal Macaque in the earlier paper.

Microscopically the older gland shows distinct advances in development from that seen in the younger one. The younger organ (fig. 2) shows a fairly

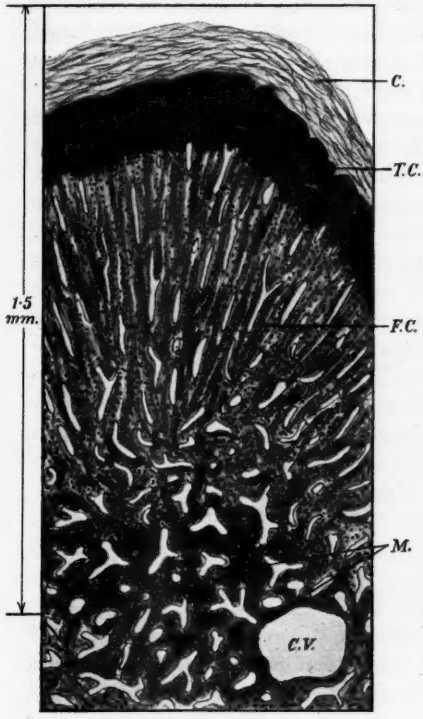

Fig. 2.

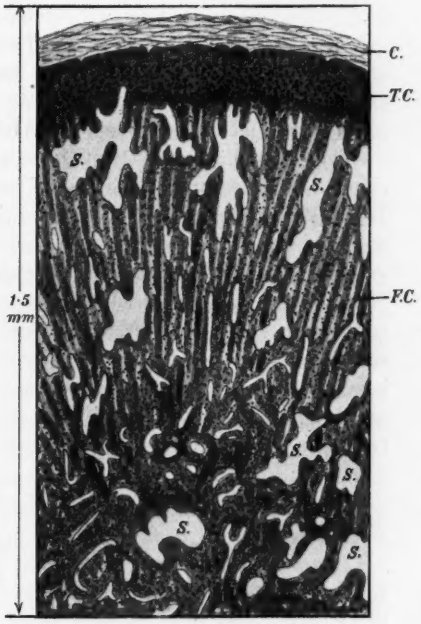

Fig. 3.

Fig. 2. Microscopic characters of the suprarenal of a foetal male *Pithecus senex vetulus*, C.R. length 72 mm. *C.* capsule; *T.C.* true cortex; *F.C.* foetal cortex; *M.* clumps of medullary (chromaffin) cells; *C.V.* central vein.

Fig. 3. Microscopic characters of the suprarenal of a foetal male *Pithecus senex vetulus*, C.R. length 96 mm. *S.S.S.* sinus-like blood spaces due to engorgement and rupture of the originally radial vessels seen in fig. 2. Other references as in fig. 2.

thick capsular investment, with processes passing therefrom into the gland substance. Under this is a zone of cortex consisting of many closely packed small cells. They do not present a glomerular arrangement, but seem to be equally dense throughout the zone. The zone takes up from one-seventh to one-tenth of the total thickness of tissue between the capsule and the central

vein. It is fairly uniform in thickness all round the organ. The remainder of the gland consists almost entirely of tissue having the appearance of "foetal cortex." This is thicker in parts than others, but has the same general structure throughout. It consists of large cells with plenty of cytoplasm, and large vesicular nuclei. These cells stain less heavily than those of the peripheral layer, but they are not degenerate at this stage. The cells are arranged in tall interlacing columns separated by large sinusoidal blood spaces connected deeply with the central vessel. In the peripheral half of the foetal cortex the vessels are long and straight. In the deeper half of the mass these same vessels are tortuous and form an anastomosing network. Immediately around the central vein are some more closely packed cells of large size arranged in clumps. These appear to be chromaffin cells and represent the commencing medulla of the gland. The clumps are separated by sinusoids.

The older gland consists of the same elements as the younger. Important changes have occurred in the "foetal cortex." The true cortex has not changed. The central cortex is larger, chiefly owing to the swelling incident on engorgement of the sinusoids. All the vessels mentioned in connection with the younger gland have become enormously dilated and are filled with blood cells. Some of the straight vessels in the peripheral part of the foetal cortex have run together to produce large irregular blood spaces, with consequent disruption of the intervening cell columns. The deeper half of the foetal cortex is even more vascular, and appears so even to the naked eye on a fresh section of the gland. There is no advance in the development of the medulla from that seen in the earlier stage described above.

(2) *Post-natal specimens*

The suprarenals in post-natal specimens of *P. senex* have been examined in immature and adult animals of both sexes. Unfortunately no stage immediately after birth was available in this species, but a stage within the first few months was examined in *P. entellus* (see below). The description of this will be given later, and it will serve to fill in an important gap in the series of *P. senex* specimens. Of the females of *P. senex* examined one specimen was pregnant, and this showed some important points in connection with the suprarenal cortex.

The youngest post-natal specimen of *P. senex* was one of the race *P. s. nestor* which inhabits the western lowland district round Colombo. The specimen was a female about one-quarter grown. It weighed 1·75 kg., and measured 232 mm. crown-rump length. Examination of the suprarenals shows them to have already assumed their characteristic adult form, though they are still relatively larger in comparison with the kidney than in the adult animal. This applies more especially to the left suprarenal. The form of the right suprarenal seems to be peculiar to this genus of monkeys, and is correlated

with the displacement of the mesogastric viscera on account of the large size and peculiar form of the stomach. The peculiarity is to be seen in all post-natal stages of the animal (cf. fig. 1 B, C). The gland is elongated in its cranio-caudal axis, the greatest measurement being from the apex of the gland caudally to the medial basal angle, which descends a considerable way towards the hilum of the right kidney. The medial third of the ventral surface of the gland is flattened or hollowed on account of the relation it bears to the inferior vena cava. The rest of the ventral surface is in relation to the liver. The basal surface is applied to the upper pole of the right kidney, and extends medially almost to the hilum. The large suprarenal vein leaves the gland from a deep fissure on the ventral aspect, near the medial border. It runs obliquely medially and caudally almost parallel to the long axis of the gland for some distance before opening into the vena cava. The left suprarenal is of normal shape, resembling the human right suprarenal, i.e. forming the outline of an equilateral triangle when viewed from the ventral aspect. It is thickest at the base, just above which it thins out rather suddenly, so that it appears that the anterior and posterior aspects of the gland had fallen together when comparison is made with the corresponding gland of the foetus. At the junction of the thick base and the thinner apical portion of the left suprarenal there is a deep transverse groove. On the ventral aspect this groove transmits the left suprarenal vein. This arrangement, together with the fact that there is a deep hollow on the basal surface of the gland, where it is related to the kidney, is responsible for converting the uniform contour of the foetal gland into the trifoliate arrangement seen in the sectioned gland of the adult. The specimen under consideration is intermediate in this respect between the foetal and the adult conditions. Apart from the groove mentioned the surface of the gland is relatively smooth. Sections of the fresh suprarenal viewed by the naked eye reveal the presence of a peripheral rim of pale cortex and a deeper stratum of darker and more friable cortex. In the centre of the gland is a dark mass of medulla containing the central vein in section. Under the microscope the pale peripheral zone is found to consist of the typical small, darkly staining cells of "true cortex." The deeper cortex consists of larger cells arranged in irregularly branching columns, and corresponds to what would be termed zona reticularis in an adult human suprarenal.

The next specimen was a half-grown male of *P. s. vetulus*. This was obtained in a jungle near Galle in the wettest part of the lowlands. It was examined immediately after death. It was larger than the female *nestor* just described, measuring 283 mm. crown-rump length. It must be borne in mind, however, that aside from sexual differences in size, this race normally exceeds *P. s. nestor* in its final adult proportions. The suprarenals therefore cannot be very much in advance of those of the specimen just described. This is borne out by the size of the kidneys, which are about the same as in the *nestor*. The suprarenals agree in shape with those of the specimen just described. More detailed microscopic structure was, however,

obtainable from the preparations made on this animal. The following is a description of the structure observed:

Under the undulating layer of fibrous tissue which forms the capsule of the gland lies a zone of very minute well-staining cells which correspond in position and appearance with the zona glomerulosa of the typical mammalian suprarenal. The cells have small darkly staining nuclei, and comparatively little cytoplasm. Their arrangement would best be described as arcuate, i.e. forming arches, the columns of which descend towards the centre of the gland. For this reason the term zona arcuata is preferable to zona glomerulosa, as has been used by Ellenberger and Trautmann (1921) in describing the suprarenal of the adult horse. In the young monkey the arches are small, and the columns supporting them are tall and thin. Neighbouring columns are connected together at the periphery by the transverse parts of the arches. Centrally, the narrow columns of small cells are continuous with the stouter columns of larger cells that form the more extensive zona fasciculata. These larger cells have much more abundant eosinophil protoplasm, vesicular nuclei, and droplets of lipoid. They form the greater bulk of the cortex accounting for about two-thirds of its total thickness all round the gland. Underneath the fasciculate zone occurs a narrow band of similar cells more closely packed, and not arranged in columns, nor as a network. They are somewhat flattened from mutual pressure, the long axes running parallel with the surface of the gland. They correspond in position with the zona reticularis of the typical mammalian suprarenal, and probably correspond therewith morphologically. The chief difference from the typical reticular zone lies in their closely packed arrangement. They form an almost solid epithelial mass, with a minimum of vessels and connective tissue intervening. The cells, however, are degenerate in appearance. In the more superficial parts of the cortex on the other hand, vessels are large and numerous. The medulla differs from the deepest parts of the cortex by its chromaffin reaction. Morphologically its cells are slightly larger, and they stain more darkly with haematoxylin. Medulla is confined to the region round the junction of the three radii of the gland substance. In the distal parts of the radii the cortex on the anterior and posterior aspects of the gland are separated by a firm band of fibrous tissue. This is continuous with a thinner band which separates medulla from cortex in the parts where the former exists. Cramer states that in the human gland this fibrous tissue represents the scar of the degenerated foetal cortex. He erroneously concludes that the structure is confined to the human organ.

In the *P. s. nestor* numbered (5) in the table, the suprarenals measured less than the size of the animal seems to warrant. This is explained by the fact that the animal had died in captivity and had been preserved by injection. This treatment had caused the organs to shrink unduly, so that adequate comparison cannot be made with the other specimens. In section, however, the glands exhibited the same structure as that just described.

The adult male specimen of *P. s. vetulus* was obtained in the jungle and

examined immediately. It weighed 4·6 kg. Its suprarenals are represented in fig. 1 C. They have the same general shape and relations as in the previous post-natal specimens, but the cranio-caudal elongation of the right gland is relatively less excessive. The right gland is but little longer in actual length than the left, but it is only half the breadth of the left. Both glands are flattened dorso-ventrally even more than in the younger specimens. The flattening is such that the medulla is reduced to a thin strip separating the much thicker cortex on the ventral side from that on the dorsal aspect of the gland. Relative to the size of the animal the suprarenals in the adult male

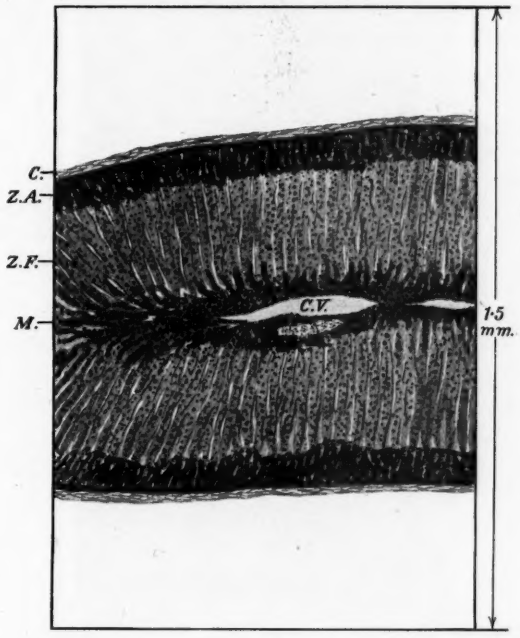

Fig. 4. Microscopic characters of suprarenal of an adult male *Pithecus senex vetulus*.

are the smallest of any of those examined. Under the microscope, the suprarenal of the adult male is seen in sagittal section to consist of two cortical plates, dorsal and ventral. These are separated in most parts of the gland merely by a band of fibrous tissue. In the centre of the gland this fibrous tissue contains the central vein, and around the wall of this occur the only islands of medullary tissue which the adult male gland possesses. The cortex is therefore the chief constituent of the suprarenal in the adult male. The details of its structure can be seen in fig. 4, and are as follows. The capsule is succeeded by a layer of zona arcuata similar to that in the previous three

specimens. It differs, however, in being of unequal depth in different parts of the section. Its average depth is the same as in the younger glands, but here and there conical projections occur on its deep surface, extending deeply among the cells of the zona fasciculata. The cells are of the usual small size, and they are clearly marked off from those of the next zone. The zona fasciculata consists of tall columns of larger cells as in the younger animals. In places its total depth is equal to that in the younger examples, but its average depth is less, and in some parts considerably less. It is, further, less vascular

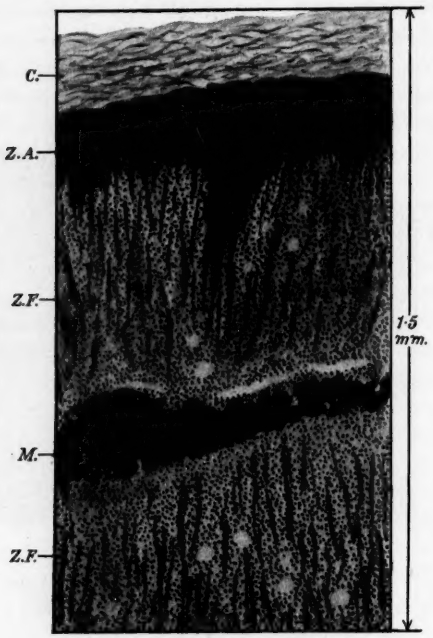

Fig. 5. Microscopic characters of the suprarenal of an adult non-pregnant female *Pithecus senex vetulus*.

than in the younger stages. There is no reticular zone whatever. This probably means that the zona reticularis disappears at some stage between the last of the younger stages described here and the adult condition. This corresponds with Howard-Miller's statements on the X-zone in the growing mouse (1927) and also with the present writer's previous findings in the adult male Macaque. Between the cortex and medulla there is a persistent fibrous tissue barrier as mentioned in the earlier stages. The medulla is restricted to the region around the central vein and does not extend into the distal parts of the organ. The central vein is flattened dorso-ventrally, so that in sagittal section it

looks long and thin. The medullary clumps are clustered all along its wall. Large tributaries of the vein are seen cut across (i) in the deepest part of the zona fasciculata and (ii) at the junction of the zona fasciculata and zona arcuata.

A non-pregnant female of *P. s. vetulus* was examined fresh at the same time as the male. The animal weighed 4·3 kg. and can thus be considered

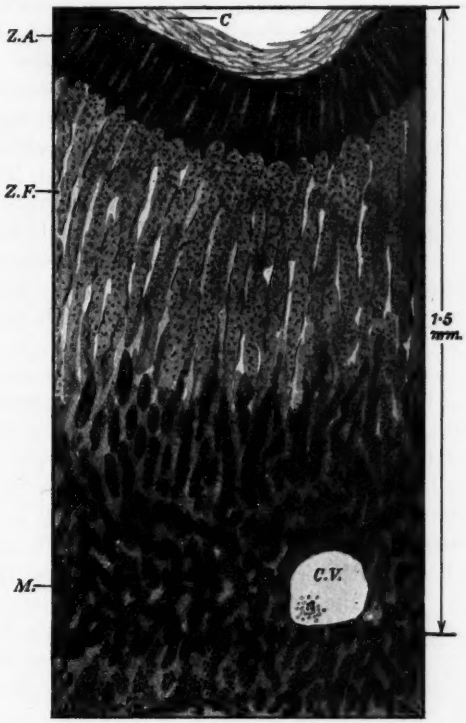

Fig. 6. Microscopic characters of the suprarenal of an adult pregnant female of *Pithecus senex vetulus*.

NOTE. Figs. 4, 5 and 6 are all drawn to the same scale. *C.* capsule; *Z.A.* zona arcuata; *Z.F.* zona fasciculata; *M.* medulla; *C.V.* central vein.

adult, and at a suitable stage for comparison with the male. The suprarenals resemble those of the male in general form and proportions, but both glands are thicker than in the male, especially towards the base. The cranio-caudal elongation of the right gland is about the same as in the male. The surface of the glands is wrinkled. Two zones of cortex are readily discerned even by the naked eye. Together they form a dorsal and a ventral plate separated by

fibrous tissue, as in the male. Each plate, however, is at least double, and in some parts more than double the thickness of the corresponding plate in the male. Microscopically (see fig. 5) the gland shows the same structures as are present in the male, but they differ in their proportions. All the zones of the cortex are thicker and the medulla is also more extensive. The zona arcuata is better developed and the arches at the top of the columns of small cells are more clearly marked. As in the male, this zone shows, in parts, conical protrusions into the zona fasciculata. These processes are more numerous and more extensive than in the male. In places they descend as much as half-way through the fasciculate zone. The zona fasciculata is roughly twice the depth of the same zone in the male. It shows a moderate lipoid reaction as in the male, but not so marked as that in the pregnant female described below. The deeper parts of the zona fasciculata show some extravasations of blood from the central vein extending into it through the medulla. There is no zona reticularis. As in the male the cortex is separated from the medulla by a sharp fibrous stratum. Medulla is not plentiful, but is more extensive than in the male. There is about twice the quantity of medulla compared with a corresponding section of the male gland.

In the pregnant female of *P. s. vetulus* the suprarenals show a remarkable hypertrophy. The female suprarenal has been shown to be normally larger than that of the male in Man and most Mammals by Schafer (1924), and it is generally believed that pregnancy calls for an increased activity of the gland. Watrin (1914) has drawn attention to an enlargement of the suprarenal in pregnant rabbits. But there is no record at present of similar changes on such a scale occurring in the suprarenal of Primates. The degree of enlargement occurring in *Pithecus* can be gathered from fig. 1. As will be seen below, the specimen here described is not an isolated instance, for the same phenomenon has been demonstrated in the pregnant female of *P. entellus*. The hypertrophy seems to advance with the pregnancy, however, for the enlargement in *P. entellus*, although this is a larger animal, was not so advanced as in *P. senex*. The latter was in a more advanced state of pregnancy than the former (corresponding to a human 5th month pregnancy compared with a 3-months pregnancy). The body weight of the female *P. senex* examined was 6·6 kg. The kidneys are slightly larger than in the male or the previous female. The suprarenals are much larger than could be explained by the increased bodily or kidney proportions. They are at least twice as large as the suprarenals of the non-pregnant female. The increase affects all the measurements, but especially the dorso-ventral one. Section reveals the enlargement to be mainly due to cortical hypertrophy, though the medulla also participates to some extent. The same cortical zones are visible to the naked eye as in the last specimen described, but both zones are greatly increased in depth, more especially the deeper zone.

Microscopically the suprarenal of the pregnant female consists of the following parts (see fig. 6). Beneath a relatively thin fibrous capsule is a zona

arcuata of similar structure and arrangement to that already described in the adult male. Here, however, the zone is about half as deep again as in the non-pregnant female. The deepening is due to an increase in the length of the columns of small cells supporting the arches. There were no irregularities on the deep aspect of this zone. It would appear, therefore, that the hypertrophy is such as to make all the arcuate cortex as thick as the thickest parts in the non-pregnant female. This gives the appearance of a uniform boundary between the zona arcuata and the zona fasciculata. The zona fasciculata consists of the usual large cells arranged in the form of sinuous columns with intervening vessels. They show a very heavy lipoid reaction with Sudan III. The zone is at least twice as thick as in the non-pregnant animal, and therefore about four times as thick as in the male.

The deepest cells of the zona fasciculata form more discrete, rounded clumps than the rest. Their lipoid reactions however are of the same intensity. The separation of cortex from medulla is irregular, forming a sinuous outline, but the boundary is marked by a fibrous lamina as in other specimens. There is no sign of a zona reticularis in the specimen examined. The medulla is more plentiful than in the non-pregnant animal. It forms an appreciable mass around the central vein, and also extends some distance into all three radii of the gland mass. This causes the organ to assume partly the shape and relative proportions of that of infancy, though not to the same degree and not to the extent of disappearance of the triradiate form of the gland.

IV. DESCRIPTIONS OF THE SUPRARENALS OF *PITHECUS ENTELLUS THERSITES*

In fig. 7 will be found representations of the suprarenals and kidneys of three specimens of *P. entellus thersites* (formerly *Semnopithecus priamus*). These are drawn to the same scale as those of *P. senex* in fig. 1, with which they should be compared. In dealing with the suprarenals in this species, and especially in forming an idea of their size in relation to total body weight, it must be borne in mind that the full-grown of this animal is on the average larger than that of any of the races of *P. senex* considered in this paper. No foetal specimens of this species have so far been available. The earliest stage is represented by a very young post-natal male. This specimen fills in a gap in the series of *P. senex* suprarenals considered above. The animal was not more than 2–3 months old. Its suprarenals were examined immediately after death. Their general form is much the same as in the young specimens of *P. senex*; but in this animal they were relatively larger, a fact apparently coupled with the juvenility of the specimen. The increase in size over the corresponding organ in the earliest post-natal *P. senex* examined, is both absolute and relative. Both glands are as large in surface outline as those of an adult male of the same species; and several times as thick. The total volume

of the infantile suprarenal therefore is many times that of the adult male. In section the suprarenal of the young male monkey presents the earliest phase in the appearance of the triradiate formation so characteristic of the adult gland. The three radii are all present, but very thick, and separated by only a slight concavity below for the upper pole of the corresponding kidney. Each radius consists of a dorsal and a ventral cortical plate, both thick, separated by a well-developed stratum of fibrous tissue, as in Man. At the junction of the three radii the cortical plates are more widely separated, for the fibrous tissue here contains the central vein, and a small modicum of medulla. Two colour zones are visible to the naked eye in the cortical plates.

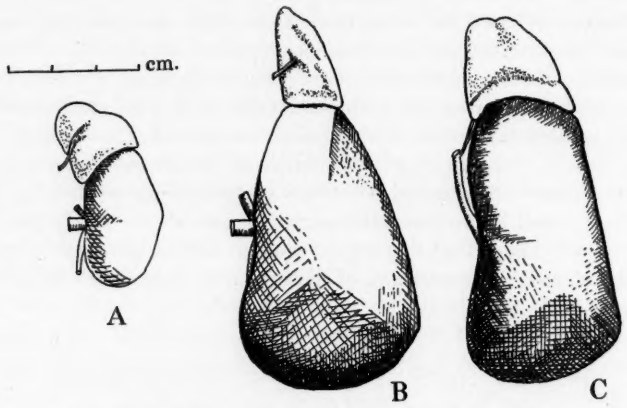

Fig. 7. Drawings of the kidneys and suprarenals of three specimens of *Pithecus entellus thersites*. All drawn to the same scale. A. Very young male. B. Adult male. C. Female in early pregnancy.

Microscopically the capsule is thin. Deep to it is a very narrow zone of very small cortical cells arranged very closely and not yet forming either arches, glomeruli or columns. This zone forms the young stage of the zona arcuata of older specimens. It is uniform in thickness throughout. The bulk of the cortex is made up chiefly of zona fasciculata lying deep to the above. It is of greater depth than the corresponding zone of the half-grown *P. senex* described earlier on, or of the adult male of either species. Deep to it again is a well-marked zona reticularis, with whose cells those of the fasciculate zone are continuous. The arrangement of the zona reticularis is that of the typical mammalian suprarenal. The whole organ is very vascular at this stage, and there are special sites of engorgement (i) in the reticular zone, (ii) in the neighbouring parts of the zona fasciculata, and (iii) near the junction of zona fasciculata and zona arcuata. There are patches in the zona reticularis showing cellular degeneration commencing. Medulla is not plentiful, but is more

abundant than in the adult male. Most of it occurs near the central vein or around its tributaries, but there is some extension of medulla, as a delicate strip, for some distance along the radii.

In an adult male *P. entellus thersites* with a body weight of 9·75 kg. and the kidneys about six times the bulk of those of the young male, the suprarenals are actually smaller. Their outline in ventral view as seen in fig. 7 is roughly the same as that of the younger animal. In thickness, however, the

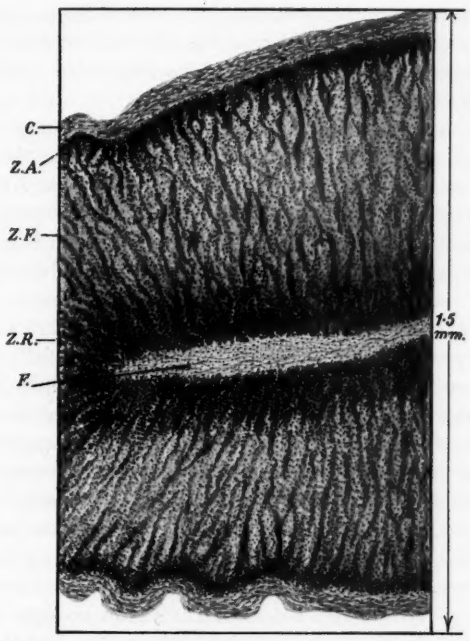

Fig. 8. Microscopic characters of the suprarenal of an infantile male *Pithecus entellus thersites* (through one radius). *C.* capsule; *Z.A.* zona arcuata; *Z.F.* zona fasciculata; *Z.R.* zona reticularis; *F.* fibrous tissue. As this section was taken through one radius, no medulla is shown. The broad band of fibrous tissue is, however, well seen.

adult gland is less than half that of the young one. The gland of the old male is therefore absolutely as well as relatively less in size than that of the young male. Sagittal section of the old gland reveals the same parts as the young section, but all the tissues are less in quantity. The gland is more flattened dorso-ventrally and the basal radii are shortened and closer together. Like the gland in the adult male *P. senex*, the main part of the organ can be described as consisting of two cortical plates, dorsal and ventral, separated at the site of the central vein by a small quantity of medulla, but elsewhere

separated only by fibrous tissue. The medulla at first sight looks more voluminous than is really the case. This is on account of the amount of space taken up by the central vein and its immediate tributaries. Actually the medulla is a sparse amount of tissue immediately surrounding these vessels. There is therefore but little effect from the chromaffin reaction to the naked eye. Microscopically the cortex shows a zona arcuata of small depth, better formed than in the young animal, but not possessing the tall columns seen in the post-natal specimens of *P. senex*. The rest of the cortex consists of zona fasciculata. Its cells are of the usual type and present the normal arrangement. They have only a moderate lipoid reaction. There is no zona reticularis, but the medulla is separated from the cortex by a very definite fibrous layer. The medulla calls for no special remark.

A third specimen of *P. e. thersites* examined was a young adult female in an early stage of pregnancy. The uterus was enlarged to the globular state, but the cervix was still hard. The animal weighed 8·6 kg. The kidneys are little inferior in size to those of the adult male, but the suprarenals are much larger, roughly about twice the total size. The left gland is normal in shape, the right has the curious cranio-caudal elongation already mentioned in connection with *P. senex*. Both glands have a wrinkled surface. Sagittal section reveals to the naked eye the same zones of cortex as in the male, but, as with *P. senex*, all the zones are deeper in the female, and especially in the pregnant female. In the present example, however, the hypertrophy of the cortex is not so advanced as in the specimen of *P. senex* described above. This fact is probably correlated with the stage of pregnancy. Microscopically the capsule is thin. The zona arcuata is well formed and has an irregular deep surface, sending long strands down into the deeper parts for some considerable distance. The zone, however, apart from these strands, consists of the arches only, there being no columnar portion as in *P. senex*. The zona fasciculata is the thickest part of the cortex. As in the pregnant female of *P. senex*, the cells of this zone show a very intense lipoid reaction. They show no signs of degeneration. Another important fact is the vascularity of the cortex. All the deeper vessels of the gland are engorged, including those of the medulla. The engorgement passes distally beyond the limits of the zona fasciculata, and the zona arcuata is very vascular all round the circumference of the gland. Large masses of blood cells are to be seen in the hollows of the arches. The deepest parts of the zona fasciculata are also very heavily injected. In parts the cells exhibit a formation similar to zona reticularis, but in other parts they are more closely packed, resembling this part in the suprarenal of the infantile male. The cortex is separated from the medulla by a fine fibrous stratum.

V. DISCUSSION

It is clear from the descriptions of the suprarenals in this series of *Pithecus* monkeys that, as in Man, there are three morphological entities to be considered, the "true cortex," the "foetal cortex" and the medulla. It is only in the case of the medulla, even in Man, that the complete story of its origin can be told. There are still many points to be cleared up with regard to the "true" and the "foetal" cortex. These two have generally been regarded as having a common origin from the cells of the genital ridge, but the differentiation of the "true" from the "foetal" cortex has not been satisfactorily studied up to the present. Lucas Keene and Hewer brought forward some evidence that the "true" and the "foetal" cortex had a different origin. Cramer has even gone so far as to suggest that "foetal cortex" is not necessarily cortex at all, either morphologically or physiologically. On physiological grounds he believes that it deserves to be classed with medulla as much as with cortex, in fact he regards it as an intermediary tissue in the physiological as well as in the topographical sense. These points cannot be settled satisfactorily until the exact origin of these tissues have been observed in the early embryonic stages.

As far as the *Pithecus* monkeys are concerned no attempt has been made here to discover the ultimate origin of the tissues. We commence with the foetal stages where the three tissues have already been laid down. As in Man, cortex is far in advance of medulla in development. Medulla at most, during foetal life, is extremely scanty, and cannot be regarded as having a very great physiological importance in these early stages. The opposite is true of cortex. The presence of such a large mass of tissue presenting, as it does, all the signs of regular activity, argues in favour of an important physiological rôle during foetal life. This applies more particularly to the "foetal cortex," which always forms the greatest part of the foetal suprarenal. True cortex, on the other hand, is less in importance, and in the earlier foetal stages shows a relatively undeveloped condition. There are, in *Pithecus*, important vascular changes occurring in the suprarenal during foetal life, more especially in the "foetal cortex." Probably, as in *Homo* and *Macacus*, the "foetal cortex" commences to degenerate, at any rate in part, before the end of foetal life, the process being continued and accompanied by vascular engorgement after birth. That the "foetal cortex" eventually completely disappears as such is the general belief, but it is a moot point whether all its cells actually disappear. It is quite probable that some of this tissue persists and forms part of the cortex of the post-natal gland. There is no evidence contrary to this view in this study of cortical development in *Pithecus*.

After birth the cortex of the suprarenal still has many phases of development to pass through. Whatever degeneration of "foetal cortex" occurs after birth in *Pithecus* monkeys, it must be a very rapid process, for in the earliest post-natal stage examined (the infantile male of *P. entellus*) "foetal cortex"

as such has disappeared, and in its place is a well-developed zona fasciculata, and a zona reticularis which already shows signs of itself degenerating. The gland as a whole, is still large, and the cortex is to be considered an important organ. The medulla, though much increased in size, and obviously in secretory activity, cannot be considered as of the same importance as the cortex. The "true" cortex of foetal life has become greatly developed, and gives rise to the zona arcuata of the post-natal gland. The cells of this zone, though still small and closely packed, are larger than in foetal glands, and show more evidence of activity. The greater part, though possibly not all, of the zona fasciculata is probably also developed from the true cortex of the foetal gland. The zona reticularis, being itself a transient structure—for it later disappears in both sexes before adult life is reached—is quite likely to be a development of the foetal cortex, and if this is the case it may be that neighbouring parts of the zona fasciculata have a similar origin. The appearances seen in the suprarenals of this series of monkeys are in favour of this view. There is no decisive evidence in the series of monkeys examined of the cells of the zona fasciculata being the product of a downgrowth from the arcuate zone. The cells seem different from the start. The cells of the arcuate zone are always small, and the columns they bud off during foetal life persist as small cells distinguishable from the fasciculate zone even in the adult. In this respect the cortex of *Pithecus* differs from that of Man and *Macacus*. In one respect, however, the two zones agree—they both possess the lipoid reaction—but so does the foetal cortex. The reaction is always heavier in cells of the fasciculate zone than in those of the arcuate zone. It is, moreover, greater during pregnancy than at other times.

The zona reticularis consists of the same type of cells as the zona fasciculata, of which most authorities consider it a part. In the youngest animals in which it is recognisable, it has the characteristic net-like arrangement, with vessels in the meshes of the net, communicating deeply with the sinusoids of the medulla. In half-grown animals the reticularis becomes more condensed, and shows signs of degeneration, the outlines of the cells becoming lost, and the cytoplasm vacuolated and ragged. Later still the zone disappears in both sexes. We have here, therefore, a transient zone similar to that described in the mouse by Howard-Miller (1927), and also corresponding to the condition already described for the male of *Macacus* by the present writer (1930). As far as *Pithecus* is concerned, there seems to be no sexual difference in the fate of the reticular zone. It disappears in both sexes. According to Cramer's hypothesis, it is possible that this transient part of the cortex is a derivative of the "foetal cortex," and some of it may be transformed into medulla. This latter part of the hypothesis, however, is very unlikely on embryological grounds.

The sexual differences in the suprarenal concern chiefly the gland of the adult monkey. It is stated in many text-books that the suprarenal of the female is enlarged during pregnancy (cf. Schafer, 1924), but it is not so widely

known that the female suprarenal is normally larger than that of the male. Kolmer (1912) is quoted by Blair Bell (*The Sex-complex*, 2nd ed. 1920, p. 13) as having claimed to have noted sexual differences in the suprarenals of rabbits; and Watrin (1914) has discussed an enlargement of the suprarenaal cortex during pregnancy in the same animal. In no animal, however, do the sexual differences in the suprarenal cortex stand out as in *Pithecus*. The normal female suprarenal is considerably larger than the male gland, the enlargement being chiefly due to the cortex, and more particularly to the zona fasciculata. This zone, moreover, tends to show a heavier lipoid reaction than in the male. To some extent the columnar part of the arcuate zone is also larger in the female than in the male. During pregnancy the normal enlargement is still further increased, the increase again affecting chiefly the zona fasciculata, which reaches double its thickness in the non-pregnant state. The columnar part of the arcuate zone is also affected during pregnancy, as shown in the figures. The enlargement of pregnancy seems to be progressive, being less well marked in early than in later stages of gestation. Such obvious enlargement has not yet been recorded for other Primates, but there seems no reason to suppose that *Pithecus* is alone in respect of this. It is highly probable that, when suitable material is examined, even the human female suprarenal will show differences similar to those described above. It is hoped, in the near future, to make some observations relative to this matter on material already existing in this department.

VI. SUMMARY AND CONCLUSIONS

1. The size, form and structure of the suprarenal glands, with particular reference to the cortex, have been described in a series of *Pithecus* monkeys of different ages and sex.

2. The foetal gland is shown to have the same size relations to the kidney as in the foetus of Man and *Macacus*. The enlargement is proved to be due to the presence of a large mass of "foetal" cortex.

3. The medulla is shown to have the same arrangement as in the human foetal gland.

4. Young post-natal glands are also shown to be large when compared with the glands of adults. In this case the enlargement is due to a deep zona fasciculata, and to the presence of a zona reticularis.

5. The zona fasciculata diminishes in depth with adult life, especially in the male. In the female it remains larger, and undergoes hypertrophy during pregnancy.

6. The zona reticularis in later childhood becomes condensed, and before adult life it disappears in both sexes.

7. The original "true cortex" of the foetal gland is transformed into a zona arcuata, consisting of parallel columns of very small cells, neighbouring columns being united superficially to form arches. This zone is sharply marked

off by the characters of its cells from the underlying zona fasciculata, but in places it dips down into the latter.

8. The possibility is mentioned that the fasciculate and reticular zones are not derived from the "true cortex" of the foetus, but by metamorphosis from the "foetal cortex."

9. It is shown that the adult female suprarenal is always larger than that of the male, due chiefly to the larger amount of both arcuate and fasciculate zones of the cortex, especially the latter.

10. The enlargement of the female gland during pregnancy is an exaggeration of the normal condition, and affects the same tissues. It progresses with the pregnancy.

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THE TOPOGRAPHY AND HISTOLOGY OF THE PARATHYROID GLANDULES IN *XENOPUS LAEVIS*

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During the past few years the exceptional suitability of the South African clawed toad, *Xenopus laevis*, for physiological investigations has been increasingly appreciated. Especially useful is its ability to withstand the severest of operative procedures, and also the power of the living animal or of its isolated organs to resist great variations in the environment.

Of particular interest to the experimental physiologist is the endocrine system of *Xenopus* which has only been carefully investigated during the last two years. Rimer (1) published accounts of the pituitary and thyroid glands, while Zwarenstein and Schrire (2) and Epstein, Gunn, Epstein and Rimer (3) elucidated the distribution and structure of the adrenal glands. The parathyroids have not hitherto been located. The need to do so has recently become more pressing in view of the large amount of work done during the last few years on the part played by the pituitary and ovaries in the calcium metabolism of *Xenopus*. The fact that the situation of the parathyroids in this animal is unknown prevented the further elucidation of the problem of the factors controlling the blood calcium, and impressed the need for investigating the whereabout of the glandules.

Amphibia are the lowest animals in which parathyroids have been found. Toldt (4) referred to the parathyroid bodies in Amphibia as "Nebenschilddrusen," a term which led to their being confused with true accessory thyroids. Maurer (5), however, recognised that they were not accessory thyroids, but homologous with the parathyroid glandules of higher vertebrates.

The following is an account of the anatomical relations and histological structure of the parathyroid glandules in *Xenopus*. In order to locate them serial sections of the head and thorax as far down as the apex of the heart were cut.

TOPOGRAPHY

The glandules lie very deeply, and in order to expose them the skin, pectoral muscles and sternum must be removed, and the heart with its large blood vessels revealed. The glandules are most easily located by reference to their relations to these blood vessels which should be clearly defined.

The sinus venosus is joined by a single inferior vena cava and right and left superior venae cavae. Each superior vena cava is seen to receive (1) the

external jugular vein passing down from the region of the ventral wall of the mouth; (2) the vena anonyma formed by the junction of the internal jugular vein and a smaller vein, the subscapularis, from the muscles of the scapula. The vena anonyma then runs downwards parallel with the musculus petrohyoideus. In this connection the nomenclature of Grobbelaar (6) has been preferred to that of Gilchrist and von Bonde (7) on both phylogenetic and embryological grounds. The superior vena cava also receives (3) the subclavian vein formed by a branch from the abdominal muscles, a branch from the skin and by the brachial vein from the arm.

The conus arteriosus is seen to divide into two branches, each of which subdivides into three arches. (1) The carotid arch, which passes laterally and is characterised by a bulbous enlargement—the carotid body. From the region of this body two arteries pass forwards. The more medial is the muscular artery (referred to as the hyothyroid artery by Rimer) which supplies the mylohyoid muscle and the thyroid gland, the lateral is the lingual artery. They sometimes have a common stem of origin which may be considered to represent the external carotid of *Rana*. Beyond the carotid body the arch continues as the internal carotid artery. (2) The systemic arch, which passes laterally and backwards on each side, and unites with its fellow of the opposite side to form the dorsal aorta. It is important to note, in connection with the precise relations of the parathyroids to be described below, that the systemic arch curves round the lateral aspect of the distal end of the processus thyroideus of the hyoid apparatus, and that as it does so it is pronouncedly kinked. (3) The pulmocutaneous arch which curves just below the systemic arch and divides into a pulmonary and a cutaneous artery.

Once the blood vessels of the region have been clearly defined localisation of the parathyroids is easy and accurate despite the fact that they are so small as to be invisible to the naked eye.

They were found to lie remarkably far down and, as in other Amphibia, at a very considerable distance from the thyroid gland.

There are two glandules on either side situated in a triangular area bounded by the carotid arch anteriorly, the systemic arch posteriorly, and the hypoglossal nerve, as it passes upward to supply the muscles of the ventral wall of the mouth, laterally. They usually lie in the lateral part of this area in a line with the carotid body anteriorly and the systemic arch at the point where it is kinked as mentioned above, posteriorly (fig. 1). The glandules are often found attached by fibrous connective tissue to either of the two last-mentioned structures.

In *Rana*, on the other hand, the parathyroids occupy a somewhat different position. They lie on the lateral side of the external jugular vein in the sinus sternalis and medial to the external carotid artery near its origin (fig. 2). It must be explained that external carotid is here used in conformity with the nomenclature of Gaupp (8) and corresponds to what most English text-books less advisedly call the lingual artery.

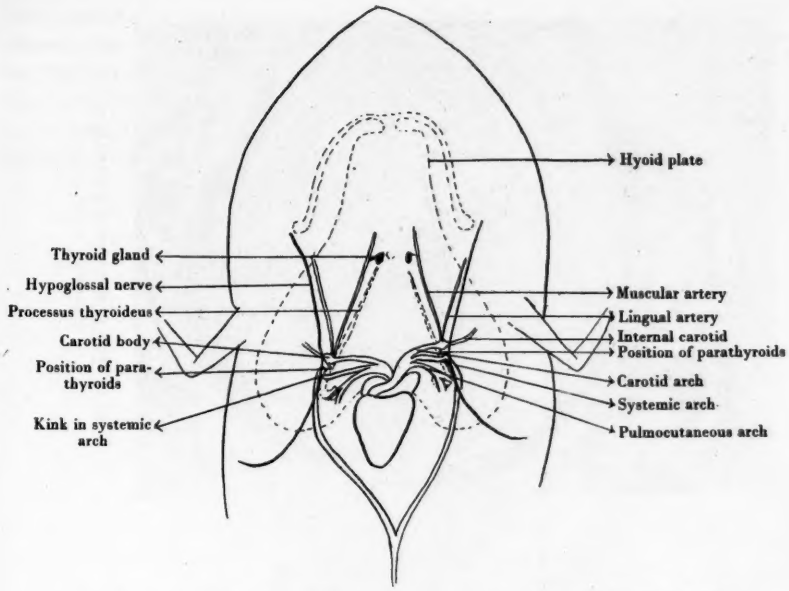

Fig. 1. Diagram showing relations of parathyroid glandules in *Xenopus laevis*.

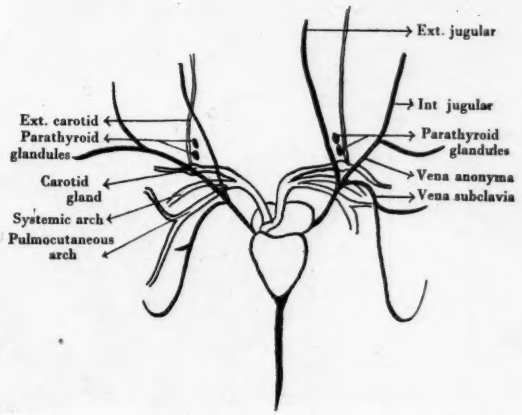

Fig. 2. Diagram of position of parathyroids in *Rana*.

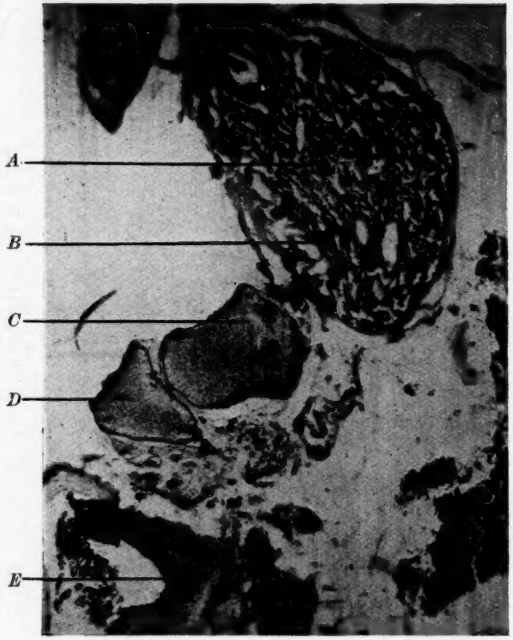

Fig. 3. Photomicrograph of sagittal section through parathyroid region in *Xenopus laevis*. × 50.
A. Carotid body; *B*. Pigment in carotid body; *C*. Antero-dorsal glandule; *D*. Postero-ventral glandule; *E*. Systemic artery.

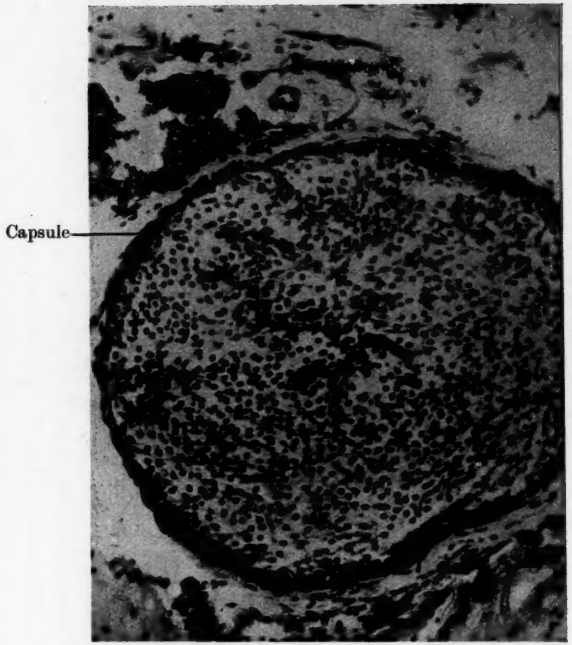

Fig. 4. High power view of a parathyroid glandule. × 200.

In *Xenopus* it was found that one glandule is generally dorsal, anterior and somewhat medial to the other, the adjacent surfaces being separated by fibrous tissue. They are both irregular bodies, the antero-dorsal glandule tending to be spheroidal and the postero-ventral one pyramidal in shape (fig. 3). Each glandule is of the order of 0·3–0·4 mm. along its greatest axis as compared with 1 mm. in other Anura generally. Occasionally only three glandules could be found, two on one side and one on the other.

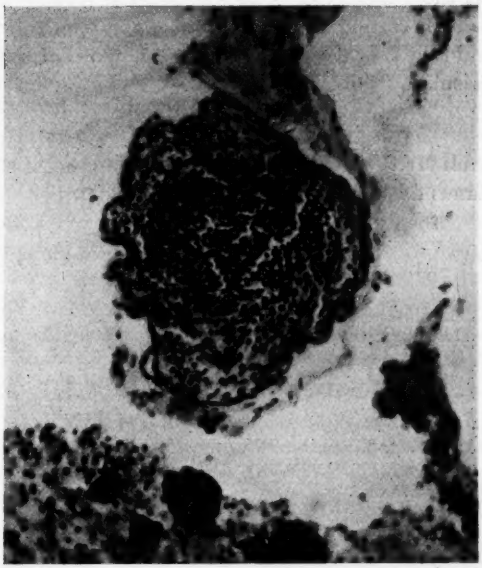

Fig. 5. Photomicrograph of a glandule which showed a whorl arrangement. × 200.

HISTOLOGY

The tissues were fixed in formalin, and some were stained with haematoxylin and eosin and others with van Gieson's stain.

Each glandule is invested in a strong compact fibrous tissue capsule which is surrounded by looser fibrous tissue continuous with the adventitia of the neighbouring blood vessels.

The structure of the glandules (fig. 4) is identical with that described for other Anura in that the interior of the body is compact and consists of epithelial cells which are closely packed especially towards the centre. Some of the cells are round, others elongated, and they contain round, spindle-shaped or elongated nuclei which stain very deeply. Some of the round cells tend to be vacuolated.

On the other hand it must be remarked that, whereas the cells of the parathyroids of other Anura are characterised by a whorl arrangement of the cells as if the body had been subjected to a process of torsion, in only a very small percentage of the parathyroids of *Xenopus* was there any suggestion of such a disposition of the cells. Fig. 5 is a photomicrograph of one such case. In the fact that it generally lacks this characteristic and in the smallness of its dimensions the parathyroids of *Xenopus* resembles more that of the Urodeles than of the Anura. In this connection it is interesting to note that Rimer finds that the pituitary of *Xenopus* essentially conforms to the salamandrine type in the incomplete separation of the pars tuberalis from the pars anterior, and that Zwarenstein and Schrire noted that the adrenal gland of *Xenopus* is essentially similar in distribution and structure to the adrenal of Urodeles.

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CARTILAGE CANALS

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INTRODUCTION

The development of cartilage and bone in the primary centres of the skeleton has been the subject of a very large number of reseârches, and the morphological aspect of the various phases is now known in great detail. Ossification of the secondary centres in the epiphysial cartilages has on the other hand attracted less attention, although the history of the growth both of the cartilage and of the bone is quite different from that in the primary centres. For whereas the cartilage of the primary centre is avascular, and is ossified by a periosteal bud which erodes the calcified cartilage, the epiphysial cartilage contains during its later growth a rich series of large blood vessels which ramify in its interior, and when ossification occurs these supply the material for the formation of the centre. It is the arrangement, development and functions of these vessels that form the subject-matter of this paper.

The existence of vessels in the epiphyses has long been known. The earlier writers are not available to me, but are quoted by Bardeen in Keibel and Mall (1), where their work is summarised in the statement that "Blood-vessels, which spring from the periosteum and from the bone-marrow, penetrate into the epiphysial cartilage long before ossification begins.... In some cartilages the blood-vessels appear in the third foetal month. In the seventh all the larger cartilaginous areas show rich vascular plexuses."

These vessels do not lie in direct contact with the cartilage, nor do the arteries and veins run independently of each other. Stoss (10) and Stump (11) have shown that the artery carrying the blood into the cartilage, the vein bringing it out and the capillary plexus between them all lie in a matrix of connective tissue which serves as a bed for their passage. The whole structure, including both the vessels and the connective tissue, is known as a cartilage canal. These canals form conspicuous branching systems in the cartilage.

The nature of the canals was studied by Eckert-Möbius (3) in the petrous temporal. He showed that their primary function is that of nutrition of large cartilages, and that where this nutrition fails degeneration and calcification of the cartilage take place, so that the canals determine the position of the centre of ossification.

Hintzsche (5, 6), working on reconstructions of the lower end of the femur and of the calcis, gave the first accurate description of the forms taken by the canals. But he found no causal connection between their position and the site of the centre of ossification which he suggests is determined by

mechanical forces, either in each individual embryo, or in the ancestors of the species. In this paper these findings are discussed in the light of studies on other bones and on other animals.

A number of special technical difficulties have to be met in the course of such a study. The canals are too small and delicate for macroscopic study, and the cartilage too opaque for study as a transparency. In cleared specimens the connective tissue of the canals is not differentiated from the cartilage, and even if the blood vessels be injected only a poor picture of the arrangement of the canals is obtained. Thus it is essential that a reconstruction model be made. The wax method was used by Hintzsche, but is unsuited to delicate branching structures. For this reason I have evolved a celluloid method which is well suited to the study, but which is so similar to that already described by Senior (6) that it is unnecessary to give a detailed description here. It may be noted that it gives accurate information about the distribution and branching of canals, but not about their thickness at any point. The drawings therefore are accurate on the first two points, but not on the third.

I have used Man as the type for this description, giving a series of reconstructions of bones in various developmental stages. Drawings from other animals have been used to illustrate certain aspects of the discussion. Under further headings are discussed the development of cartilage canals, their relation to epiphysial ossification, and their functions, while a separate section is added on the canals which pass from the epiphysial cartilage into the shaft, as the presence or absence of these has been a matter of interest in clinical studies.

CARTILAGE CANALS IN MAN

Fig. 1 shows a second phalanx from a five months' foetus, in which the cartilage canals have just formed and are in their earliest stage of development. The model is drawn so that the canals are seen at *A*, *A* as solid objects inside the transparent cartilage. Each forms a short unbranched stump. There are none at the distal end of the bone.

An examination of a section passing through one of the eight canals shows it to contain a core of loose young connective tissue continuous with that of the perichondrium. Embedded in this tissue is a small arteriole, continuous externally with the circulus vasculosus around the epiphysis.

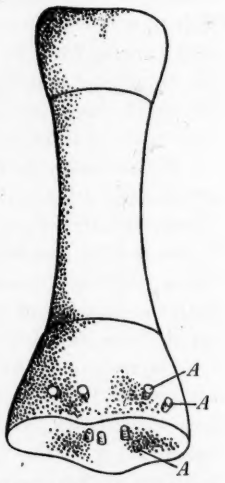

Fig. 1. Celluloid reconstruction of a second phalanx from a five months' human foetus.

Investigation of a first metatarsal bone from a six months' foetus was made. At each end is a series of canals, more advanced in development than those seen in fig. 1. The canals have assumed a simple branched form. These simple

canals are characteristic of epiphyses at this early stage of development. The canals at the distal end of the same bone are of interest, for the cartilage there is ossified from the shaft and not from an epiphysial centre. As the bone of the shaft encroaches on the cartilage, reducing it to a thin articular plate, the canals disappear. Thus the presence of cartilage canals in cartilage is not necessarily connected with the processes of epiphysial ossification.

Fig. 2 shows the two halves of the head of a fibula from a six months' foetus. In this specimen the canals have already reached their greatest diversity of form, and it may be conveniently used as a type for their description.

At *A*, *A* are *simple unbranched canals*, similar to those of the preceding figure.

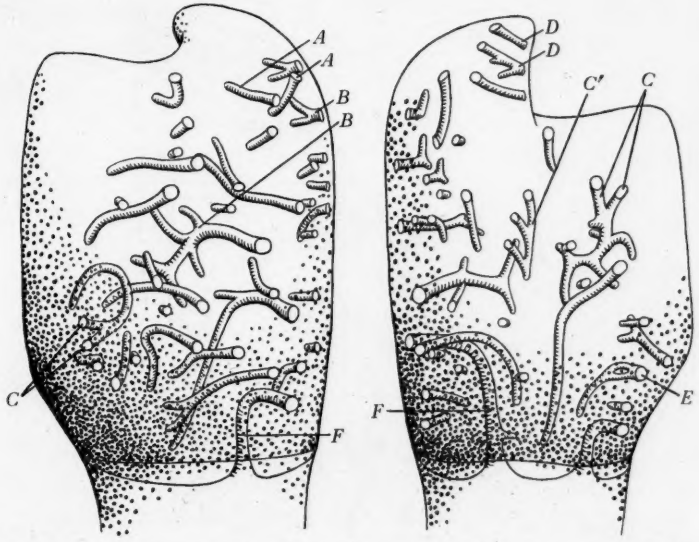

Fig. 2. Celluloid reconstruction of the upper end of the fibula of a six months' foetus.

At *B*, *B* are *simple branched canals*.

At *C*, *C* are canals either branched or unbranched which arise from the perichondrium by two separate roots, but these roots join soon after entering the cartilage. In no case does this union occur deeply within the cartilage. At *C'* there is a similar canal arising by three separate roots. These may be called *double and multiple rooted canals*.

At *D*, *D* are canals which pass directly through a projection of the cartilage from one side to the other. They occur only in those parts of the cartilage which are drawn out into projecting tongues. They may be termed *tunnel canals*.

At *E* is a canal which breaks into two divisions joining later to form again a single canal. Only one of this type occurs in this specimen. They are never common, but another is shown in fig. 4. I name these structures *divided canals*.

It may be noted in passing that these double-rooted, tunnel and subdivided canals are the only structures resembling anastomoses ever seen in epiphyses. There are no anastomoses between separate canals in the interior of the cartilage. Thus the rich vascular plexuses and the anastomoses spoken of by Bardeen (1) and Stump (11) have not been observed to occur. Their absence is demonstrated very clearly by complete reconstructions of the canal systems from serial sections. A study of separate sections gives a strong impression of rich anastomoses.

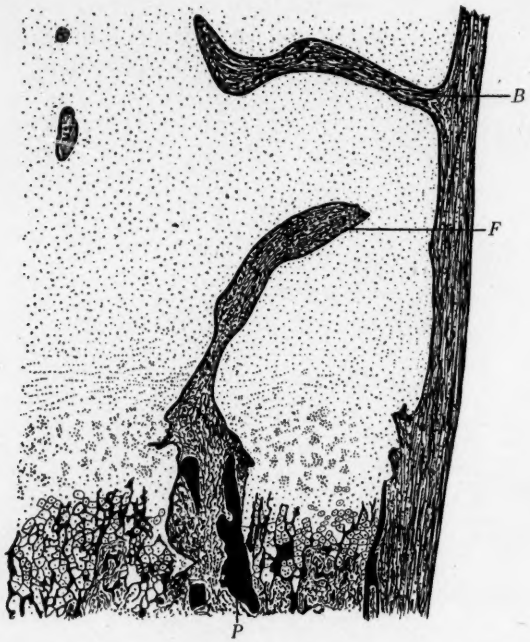

Fig. 3. Section from the fibula reconstructed in fig. 2, showing the entrance of a simple canal and the passage of a communicating canal into the shaft.

Finally at *F*, *F* are canals which, entering the epiphysis from the perichondrium, turn downwards and become continuous with the marrow spaces of the shaft. These may be called *communicating canals*.

Fig. 3 shows a section from the head of the fibula which has just been described. At *B* is seen the entry of a simple canal into the cartilage. At *F* a communicating canal passes into the shaft through the metaphysial plate of growth cartilage. The disturbance of the cartilage columns as the canal passes through is well seen. The connective tissue core of the canal is continuous from the perichondrium to the young marrow of the shaft. In the mouth of the canal is a mass of bone *P* which has ossified in the connective tissue. As this mass

has ossified in membrane it differs in texture from the cartilage bone of the shaft around it.

Fig. 4 shows the upper part of a femur separated from the rest of the bone by a horizontal cut so that the upper part of the head and the great trochanter are seen from above.

The femur is in the same general stage of canal development as the fibula shown in fig. 2, and all the types of canal occurring there are found in the femur. This reconstruction showed the blood supply to the head of the femur in the developing human bone. A well-developed series of canals enter the carti-

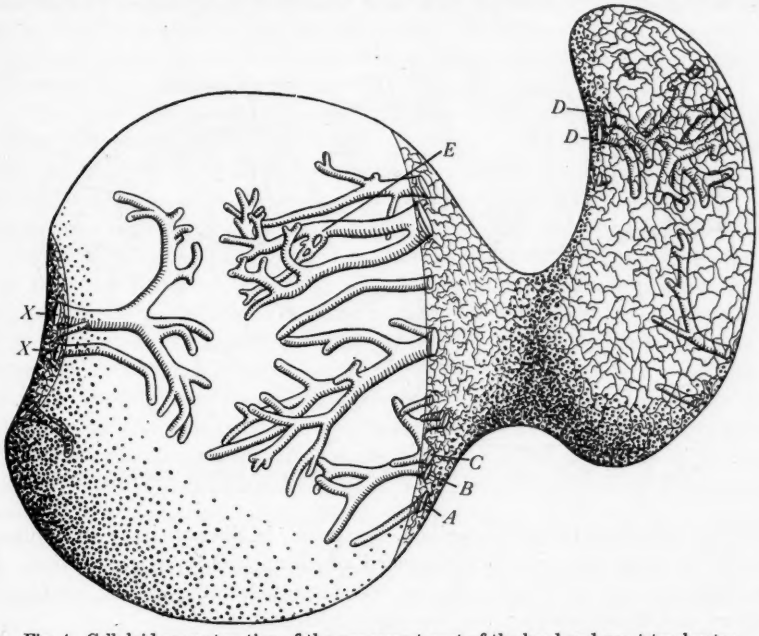

Fig. 4. Celluloid reconstruction of the uppermost part of the head and great trochanter of a femur from a six months' human foetus.

lage from the ligamentum teres. Thus at least at this stage in development the round ligament conveys a blood supply to the head of the femur. In the late foetus a considerable zone of the cartilage is supplied by blood carried by this route.

The clear figures given by Walmsley (13) bring out the fact that this supply from the ligamentum teres rapidly diminishes in extent, so that in his earliest specimen, from a child two years of age, it has become negligible, while in the adult it is confined to the connective tissue in the fossa for the ligament, and does not enter the bone. These findings are confirmed by my own study of the femur after ossification has taken place in the head, for though the group

of canals from the ligamentum teres is still clearly recognisable in a child of eighteen months, it is much reduced in proportion to the other systems.

Investigation of the same specimen also brought out clearly the sharp separation of the teres group of canals from the remainder. There are no anastomoses between the teres group and the remainder, nor do they interdigitate, being separated by an avascular lamina of cartilage lying between the two groups. Such avascular laminae occur commonly in epiphyses and will be further considered in relation to centres of ossification.

Fig. 5 shows the cartilage canals in a navicular bone before ossification sets in. It is given as an example of a short bone possessing canals, to compare

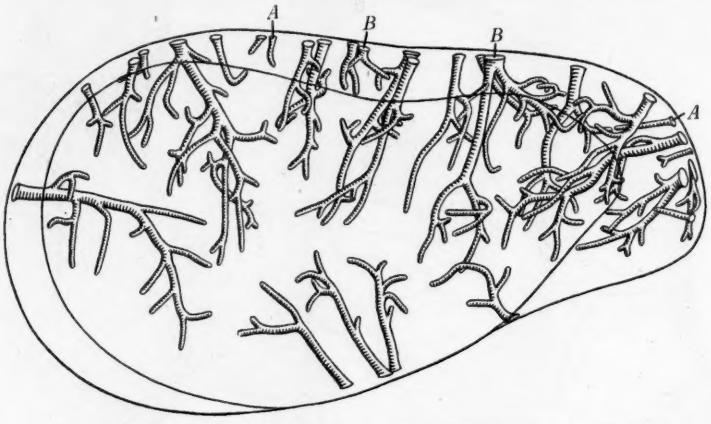

Fig. 5. Celluloid model of a navicular bone from a six months' human foetus.

with the epiphyses already described. The canals in the two cases are similar, but in this case only simple unbranched and branched types are present. A well-marked avascular lamina lies between the canals entering from the dorsal surface and those entering from the plantar surface.

Similar canals occur in other short bones. They have been reconstructed in the calcis by Hintzsche (6), and a series showing vascularisation of this bone and of the talus has been shown recently by Hurrell (7). A microphotograph of vessels in a cleared vertebra has been published by Todd (12).

All the types of cartilage canals that I have observed before the ossification centres appear have now been described and named.

In the earliest stages there are only simple unbranched stumps present, then the branched forms appear, and finally the more complex types. The problem of their development may now be considered.

THEORY OF THE FORMATION OF CARTILAGE CANALS

The generally accepted theory of the formation of cartilage canals was advanced by Stump(11). He emphasises the importance of the primitive connective tissue cells contained in the canals. These, he says, grow into the cartilage mass from the subperichondrial zone along channels which develop by solution of the chondromucin. This statement is based on the absence of chondromucin from the cartilage in the immediate vicinity of the canals, and on the presence within the canals of loose cells which he interprets as cartilage cells freed by solution of the cartilage matrix. This theory of the formation of cartilage canals by an active growth inwards may be called the *theory of invasion*. It is further supported by the work of Hintzsche(5).

The histological facts advanced by Stump are confirmed by a study of my series, but neither of the two pieces of evidence given can be taken as supporting the theory of invasion. For in the group of canals entering the femur from the ligamentum teres both the absence of chondromucin and the presence of the cells under discussion are found, although these canals are known to be undergoing regression in a child of eighteen months. Hence the two facts advanced are not evidence of active growth, and still less of invasion by cartilage canals.

Again, when cartilage is replaced by bone during growth, its cells undergo a preliminary multiplication and enlargement, and the matrix between the cells is calcified. Cartilage which has not undergone these preliminary changes is never eroded by the young connective tissue of the marrow spaces of the shaft or by the tissues of the perichondrium. When cartilage is destroyed directly, without multiplication, enlargement or calcification (as in the tadpole's tail at metamorphosis) the process is carried out by an army of leucocytes and not by young connective tissue. No such army of leucocytes is present around the young cartilage. So it is most unlikely that the theory of invasion is valid, and an alternative *theory of inclusion* is here suggested.

It is agreed that the cartilage of the epiphyses grows largely by change of the connective tissue cells of the perichondrium into cartilage cells, which add themselves to the periphery of the cartilage mass. Thus the perichondrium forms a zone of active growth around the epiphysis. In the process of change from connective tissue to cartilage the capillaries of the perichondrium are obliterated and their remains included in the cartilage.

But when the cartilage has attained a certain bulk all the blood vessels of the perichondrium are no longer destroyed. Some of the vascular loops, presumably the "strongest," persist, each surrounded by a zone of unchanged connective tissue derived from the perichondrium. By the formation of cartilage in the perichondrium around them these loops and their connective tissue matrix come to project into the mass of cartilage as short stumps—the beginnings of cartilage canals.

A continuation of these processes may lead to the inclusion within the

cartilage of the arteriole and venule supplying several originally distinct cartilage canals, so that they now form offshoots of a single branched canal.

The phenomena noted by Stump may conveniently be considered here. The absence of chondromucin from the immediate vicinity of the canals is paralleled by its absence from the cartilage immediately underlying the perichondrium. It would appear that chondromucin depends for its formation on the absence of a vascular supply near by, so that it is not formed near the perichondrium or near the cartilage canals.

In a section from the navicular bone already described a canal was seen outlined by deeply staining boundaries, but containing nothing but ordinary cartilage cells similar to those outside it, except at one point where a few connective tissue cells are seen. Similar observations were made by Stump. These few cells, however, can hardly be held responsible for the formation of the whole cartilage canal by solution of the chondromucin. It is more probable that this structure is the remains of a canal whose vessels have become obliterated during growth, the connective tissue matrix being transformed into cartilage in just the same way as the connective tissue of the perichondrium is transformed. Thus, whereas Stump believes the presence of cartilage cells within a canal to be evidence of its active growth, I believe it to be evidence of its retrogression.

This obliteration of cartilage canals during growth is a phenomenon of common occurrence. It has already been described in the distal end of the first metatarsal, where there is a rich development of the canals in the young bone, but since there is no bony epiphysis for them to supply, they disappear in later development. In the femur again, the group supplying the head of the femur from the ligamentum teres is obliterated during development. The process will be noted again in the description, which follows, of the history of double-rooted, tunnel and communicating canals.

Fig. 6 shows the probable origin of several varieties of cartilage canal. Each depends on the pre-existing arrangement of the blood vessels in the perichondrium. Thus the double-rooted canal of diagram 1, A, B and C owes its origin to the inclusion of a capillary group supplied by an arteriole which is in turn derived from the point of anastomosis of two separate arterioles, both of which become included within the cartilage. By obliteration of one of these the canal becomes single rooted again before the two roots have sunk deep into the cartilage.

The tunnel canal of diagram 2 is developed by inclusion of vessels within a growing tip of cartilage. Here again the canal is obliterated at its weakest point, forming two simple canals.

The subdivided canal of diagram 3 is formed in a way similar to that of the double-rooted canal, but here the two separate arterioles are derived from a common trunk, which is eventually included to form the stem of the canal.

The development of communicating canals has attracted some attention owing to their supposed connection with the ossification of the epiphysial

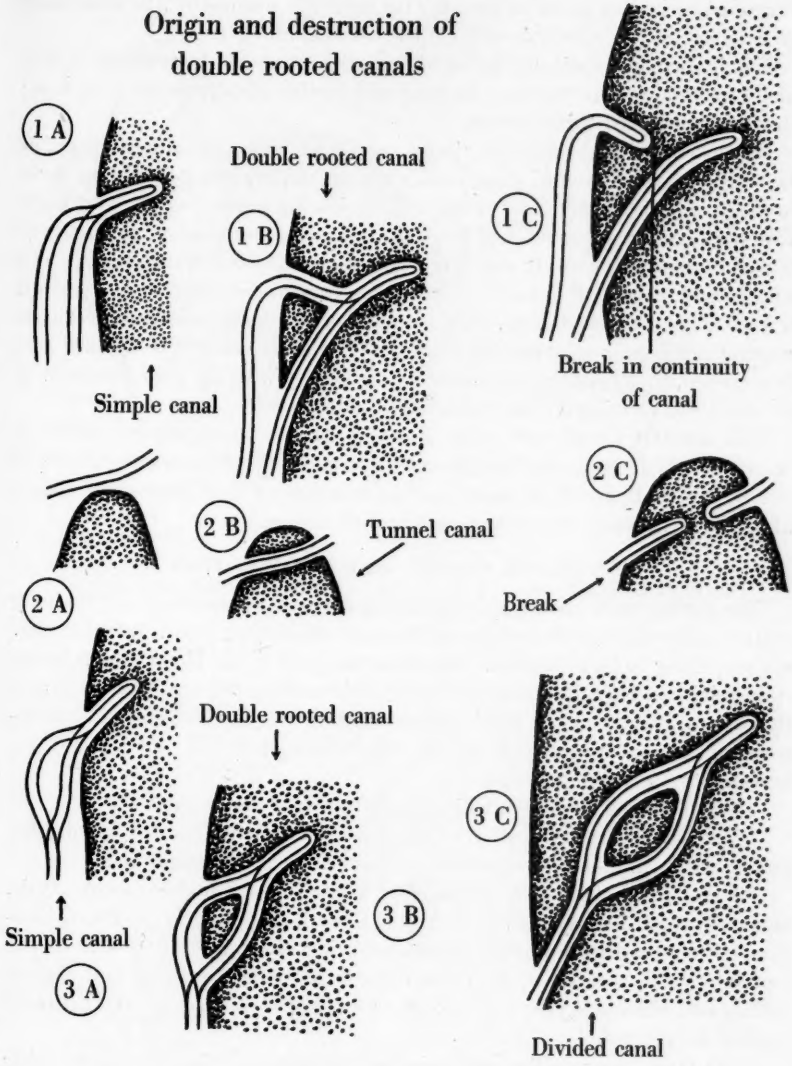

Fig. 6. Diagram showing the formation of varieties of cartilage canal.

centres. Parsons (8), who gives a good figure of these structures in the deerlet (*Tragulus*), describes them as growing up from the marrow of the shaft into the cartilage of the epiphysis to form the ossification centre.

If this theory of their development were true it should be possible to find canals springing from the bone marrow and ending blindly in the cartilage; I have not observed this to occur.

On the other hand numerous simple canals are present in the cartilage, at the stages before communicating canals are developed, and it is among these simple ones that the precursor of the communicating canals ought to be found. Now the cartilage lying nearest the shaft is undergoing changes preparatory to replacement by bone. It undergoes the processes of cell multiplication and enlargement, calcification and erosion by the young bone marrow as described in all text-books of histology. If the end of a simple canal should lie in the growing cartilage it may persist while the cartilage around it is calcified and then eroded, thus coming into secondary continuity with the young marrow of the shaft and forming a communicating canal.

This account agrees with that given by Hintzsche (6), but he describes processes which grow up from the shaft to meet the downwardly directed canals, which I would interpret as the remains of communicating canals which have become constricted and broken across.

CARTILAGE CANALS AND OSSIFICATION

The earlier work on the epiphyses was directed to the study of the bony centres rather than to that of the cartilages in which they grow. It is therefore not surprising to find that more attention was paid to the blood vessels in the epiphysial cartilages in connection with their ossification, e.g. Parsons (8) and Bardeen (1). Hintzsche (6) paid particular attention to this point in his reconstructions of the lower end of the femur, but did not extend his investigations to other bones.

Two specimens from Man will serve as types for this study.

Fig. 7 shows a thick section of the lower end of the femur of a full-time foetus, with a well-developed centre of ossification in the epiphysis.

At *A*, *B*, and *C* are seen unbranched, branched and double-rooted canals, similar to those already described. Any of these, if they impinge on the ossification centre, may form *nutrient canals* carrying blood vessels to it from the perichondrium, seen at *P*, *P*. These enter from both the dorsal and ventral surfaces of the epiphysis, the two groups being separated by the articular surface for the patella.

At *Q*, *Q* are very peculiar canals similar in structure to the others but arising from the centre of ossification, and not from the perichondrium as do all other canals. These may be called *centrifugal canals*.

Communicating canals stage completely absent in this specimen.

Fig. 8 shows the upper end of a femur in which the centre of ossification of the head is well formed, but the great trochanter is as yet unossified.

Fig. 7. Celluloid reconstruction of a thick section from the lower end of the femur of a full-time human foetus.

Fig. 8. Celluloid reconstruction of a thick section of the upper end of the femur from a child of eighteen months.

The bony centre lies between and is supplied by two groups of canals, the one entering from below the head and the other from the groove between the head and the great trochanter. This latter system, *C'*, appears to consist of separate anastomosing canals, but I believe it to be a very complicated form of multiple rooted canal. No centrifugal canals spring from the centre.

At *X* a few canals are seen entering from the ligamentum teres. They penetrate only a small part of the cartilage, and they play no part in the supply of the bony centre.

From these two figures it will be seen that there can be no possibility of the osteoblasts of the epiphysis being derived from periosteal buds growing up from the bone marrow of the shaft, for at the time of ossification all communications between the shaft and the epiphysis have disappeared. It is highly probable that they are derived from the young connective tissue of the cartilage canals, just as the osteoblasts of the shaft are derived from the young connective tissue of the perichondrium. The connective tissues of the canals and the perichondrium are exactly similar and are continuous with one another.

THE POSITION OF THE OSSIFICATION CENTRE WITHIN THE CARTILAGE OF THE EPIPHYSIS

Here there are two sharply divided schools of thought. Parsons (8) working on epiphyses, Carey (2) on the primary centre of the femur in pig embryos, and Eckert-Möbius (3) on the cartilage canals of the temporal bone, support the older view that the degeneration of cartilage which precedes the formation of a centre of ossification is a result of a lack of nutrition of the cartilage. Hintzsche (6), however, in his reconstructions of the lower end of the femur, could find no difference between the nutrition of the site of ossification and that of many other parts of the cartilage. so that he could not consider lack of nutrition as a cause of degeneration. He suggests instead the mechanical effect of the patella as it glides over the femur, working either directly on the foetus itself or more probably through its ancestors. But it will now be shown that the ossification centre always appears in an avascular zone between two sets of canals, so that its position is probably dependent on that of the canals.

For this purpose it is necessary to study the arrangement of the cartilage canals in well-developed epiphyses. Man is an unsuitable subject for this, since the cartilages at the time of ossification are too large and the canals too complicated for extensive reconstruction. I have therefore used cats of suitable ages as a basis for the work, and the results are later confirmed for Man.

Figs. 9 and 10 show the major parts of the upper ends of the femora of two kittens aged four and ten days respectively, one before ossification takes place and one after. The simplicity of the arrangement of the canals and the convenient size of the specimens make them good material for study.

In fig. 9 the canals are divided into groups *M*, *N* and *O*, entering the femur from the underside of the neck, from the groove between the head and the

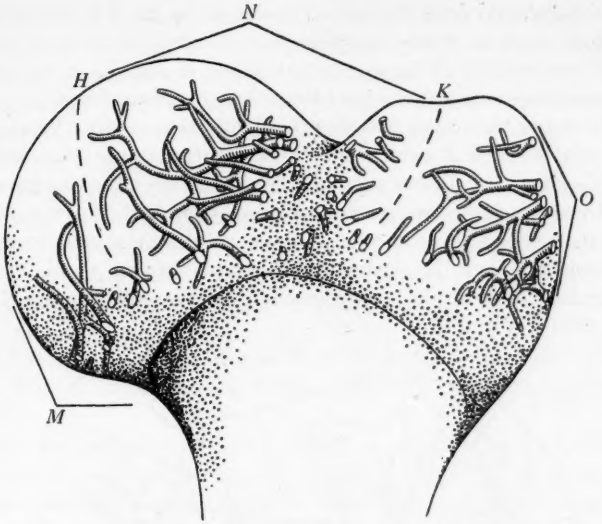

Fig. 9. Celluloid reconstruction of the major part of the femur of a four days old cat.

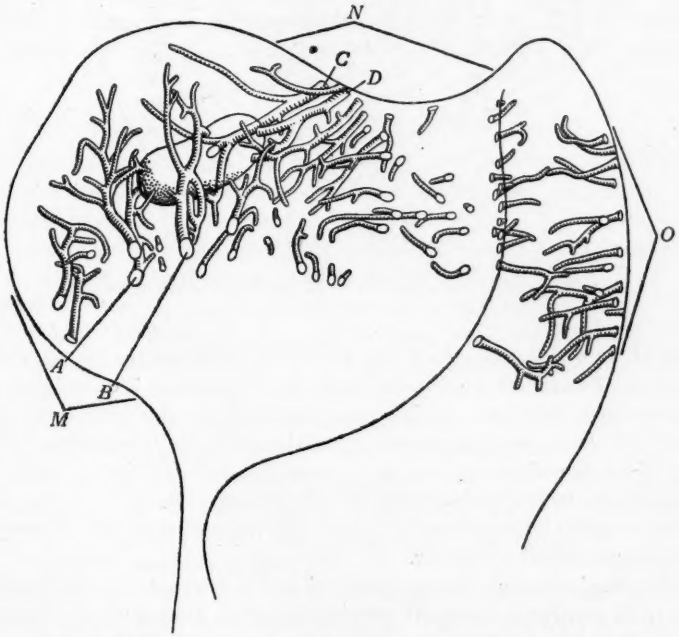

Fig. 10. Celluloid reconstruction of the major part of the upper end of the femur of a ten days old cat.

great trochanter, and from the lateral aspect of the great trochanter, respectively. Each of these groups supplies its own block of tissue and they are separated from each other by avascular laminae *H* and *K*. In the cat at this stage there are no canals springing from the ligamentum teres.

Fig. 10 shows the canals entering the ossification centre. From group *M* enter the canals *A* and *B*, from group *N* the canals *C* and *D*; that is the centre occupies the site of the former avascular lamina between the two groups and is supplied by canals from both groups. A comparison with Fig. 8 shows that in Man also the centre arises between and is supplied by the same two groups of canals, the group from the ligamentum teres playing no part in the supply. The centre for the great trochanter arises in the avascular lamina *K* between the canal groups *N* and *O*.

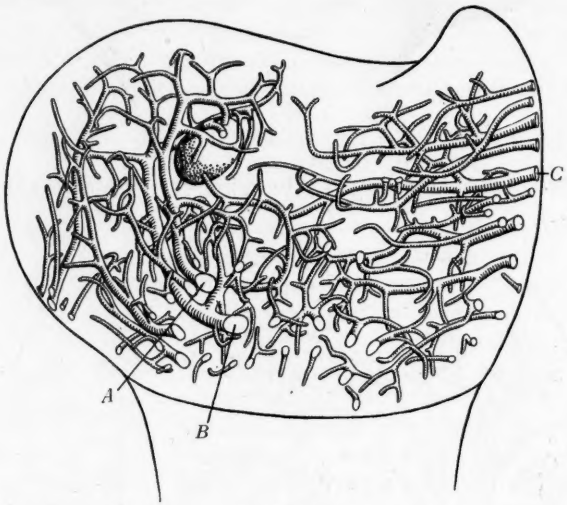

Fig. 11. Celluloid reconstruction of the major part of the upper end of the humerus of a four days old cat.

Fig. 11 shows the major part of a kitten's humerus with a young centre of ossification. I was guided in the choice of this specimen by Parsons' statement that a centre is present in a kitten of three days. In this bone the articular surface for the shoulder-joint comes as far laterally as the tendons inserted into the greater tuberosity, and the group roughly corresponding to the middle group *N* of the femur is much reduced. Their place is taken by a large group entering from the lateral aspect of the greater tuberosity, roughly corresponding to the group *O* of the femur.

The centre is supplied by two canals *A* and *B* entering from the lower part of the neck and by one canal *C* entering laterally. Here again the centre has arisen in the avascular lamina separating two groups of canals.

Finally in the lower end of the human femur already described the centre arises in a similar avascular lamina between two groups of canals separated at their entry by the articular surface for the patella.

Thus in all these cases the bony centre arises in an avascular lamina, and it is highly probable that it always does so. The next step is to show the nature of the avascular lamina itself.

Several stages in the development of an ossification centre for an epiphysis, and its relation to cartilage canals can be distinguished. In the beginning the cartilage exists before canals are present; next, the canals are developed on both sides of the cartilage leaving a clear space—the avascular lamina—between the two groups roughly corresponding in position with the cartilage mass before canals are present.

This is followed by calcification of the central part of the avascular lamina, which is at once the oldest and the least well nourished part of the cartilage.

Finally a bony centre supplied by nutrient canals from both sides of the original avascular lamina replaces the area of calcified cartilage. The severed ends of ordinary canals cut in two by the developing ossification centre may be the source of the centrifugal canals. The stems of these canals persist as nutrient canals, while their distal extremities now form centrifugal canals.

Thus the cartilage canals not only give origin to the osteoblasts and marrow of the epiphysial centre and carry the blood supply to and from the centre, but also determine by their distribution the position where the centre appears.

COMMUNICATING CANALS

The communicating canals were among the first structures in epiphyses to attract the attention of anatomists, and interest in them, rather than in the other types of canal, has persisted to the present day.

I have already mentioned that Parsons (8) described them as osteogenic buds growing up from the shaft to form the centre of the epiphysis. They are described in a similar way by Bardeen (1), but here canals passing into the cartilage from the perichondrium are also mentioned. It is now recognised that the perichondrium is the source of all the canals, so that Stump (11) for instance does not mention the communicating canals.

On the clinical side the communicating canals have attracted attention because they offer a possible path for injections passing from the shaft to the epiphysis or *vice versa*. Injection of the vessels in the canals has been carried out by certain authors whose work is not available to me but who are mentioned by Harris (4). Strangely enough Harris mentions the canals only to deny their very existence in any normal bone.

A good example of an early communicating canal has already been given in a human fibula from a six months' foetus. For comparison, I include here an example in a three weeks old dog.

Fig. 12 shows a section of a communicating canal from the femur of a three weeks' pup. It demonstrates the continuity of the connective tissue of the canal with the young marrow of the shaft, just as in the human fibula already described. Further, it shows the disturbance of the arrangement of the cells of the surrounding cartilage and the persistence of a sheath of hyaline cartilage around the canal projecting for a considerable distance into the shaft. If calcification of cartilage is dependent on a lack of nutrition, as suggested by Parsons (8), it would appear that the nutrition afforded by the canal has pre-

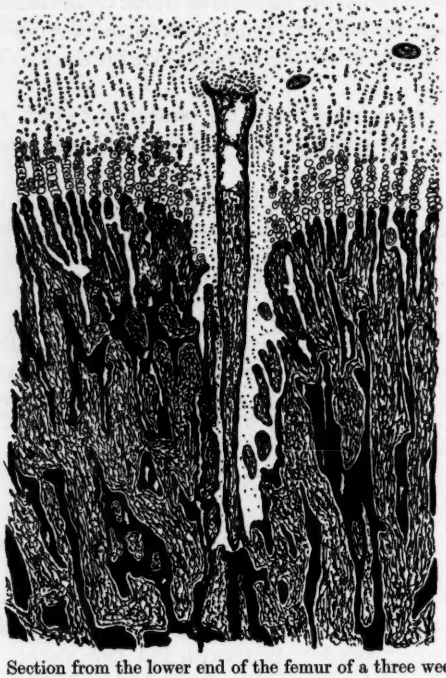

Fig. 12. Section from the lower end of the femur of a three weeks' pup, showing a communicating canal.

vented the calcification and destruction of a thin shell of cartilage around the canal, so that it hangs like a stalactite into the young bone.

This is the only well-formed communicating canal in the lower end of the femur of this pup, and there are none at all in the upper end of the tibia. It has already been mentioned that in Man the communicating canals disappear from the epiphysis soon after the centre becomes ossified, and no doubt this canal, the last of its kind in the pup's epiphysis, would soon have been obliterated had the animal lived.

The history of these communicating canals might be presented as follows. Following on an earlier phase when only simple canals are present, a later

stage ensues when the ends of the simple canals become continuous with the marrow of the shaft as described in an earlier section.

When an ossification centre develops, the canals lose their communications with the shaft, so that they now behave as simple canals, forming nutrient and centrifugal canals as the ossification centre breaks them up. This is what occurs in Man.

If the communication with the shaft should fail to be broken before the canal is split into a nutrient and a centrifugal portion, the latter will form a *centrifugal communicating canal*, that is a canal passing directly from the bone marrow of the shaft to that of the epiphysial centre. That such connections can

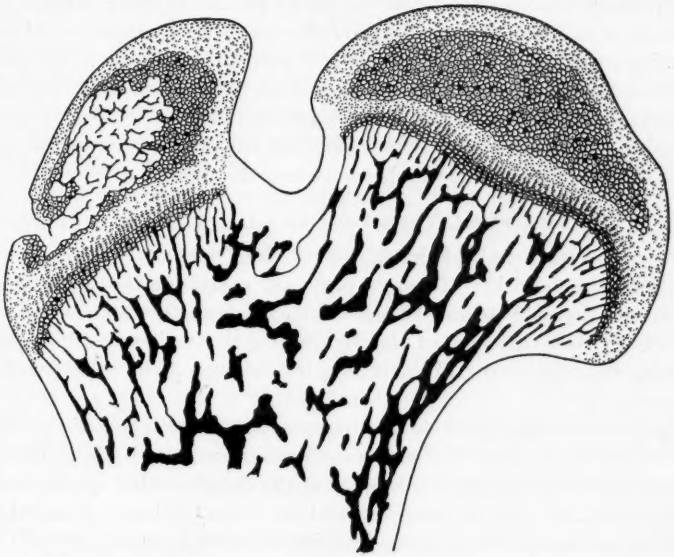

Fig. 13. Section of the upper end of the femur of a rat aged four weeks.

actually occur is shown by Parsons' figures of a deerlet in which numerous communicating canals are shown in an epiphysis in which there is already a well-developed centre of ossification. It is probably these structures which have given rise to the misconception that osteogenic buds grow up from the shaft into the epiphysis, giving rise to the centre of ossification.

EPIPHYSIAL OSSIFICATION WITHOUT CARTILAGE CANALS

This section deals with a type of epiphysial ossification which is fundamentally different from that already described. It is introduced into this paper because by its contrast with more familiar processes light is thrown on the functions of cartilage canals.

Fig. 13 shows the upper end of the femur of a young rat. The head is still

completely cartilaginous, though the centre for the great trochanter has already appeared, a reversal of the sequence found in most Mammals.

In the head a large cap of calcified cartilage divides the hyaline cartilage into a covering of articular cartilage and a metaphysial plate of growing cartilage. The great trochanter also shows a mass of calcified cartilage, but in this case the mass is eroded by young bone marrow. This marrow communicates with the perichondrium at only one point, through which passes its whole vascular supply, indicating that ossification has been brought about by a single osteogenic bud from the perichondrium. There are no cartilage canals.

This kind of epiphysial ossification can best be compared to the ossification of the primary centres of the shafts of the long bones in other animals. In the large mass of calcified cartilage formed before ossification occurs, in the absence of cartilage canals, and in the activity of a single osteogenic bud, epiphysial ossification in the rat resembles primary ossification in the larger animals.

Having studied this example, which proves that an epiphysis can develop and ossify without the formation of cartilage canals, we may now proceed to discuss the functions of the canals where they do occur.

THE FUNCTIONS OF CARTILAGE CANALS

The earlier workers held that the function of the cartilage canals was the formation and nutrition of bony epiphysial centres, although it was well known that they are present in the cartilage long before ossification occurs. Todd (12) criticised this point of view by showing that ossification does not occur primarily along the course of the canals, but he suggests no other function for the canals.

I have already brought evidence to prove that there is no intimate connection between the formation of canals and ossification, quoting both the human first metatarsal, where the canals occur at the distal end but are not followed by ossification, and the rat where ossification occurs but is not preceded by the formation of canals. The primary function of cartilage canals must, I think, be studied in epiphyses which are still in the cartilaginous stage.

Every large block of cartilage has its cartilage canals: no small block has them. In Man, for example, all epiphyses are provided with cartilage canals; whereas in the rat there are no canals. In Man the thin cartilages of the larynx have no canals; whereas in the ox, whose larygngeal cartilages are thick, there is a rich canal system. The primary function of cartilage canals is therefore the nutrition of cartilages too large to be supplied by diffusion of nutriment through their substance.

As already mentioned, Parsons has suggested that lack of nutriment leads to calcification of cartilage. In supplying this nutriment the canals prevent the occurrence of premature calcification. Thus their presence retards rather than hastens the onset of ossification.

The structure of the contents and walls of the canals is exactly similar to that of the perichondrium and the cartilage underlying it, so that the two

structures might be expected to have similar functions. Apart from nutrition the most important function of the perichondrium is the addition of new cartilage cells to the growing epiphysis. This has been shown to occur in the case of the canals, if my interpretation of the observations made by Stump, as given above, is correct. How important this contribution to new cartilage formation may be, I have no means of judging.

Thus the primary function of the canals is that of nutrition. They are not necessary to epiphysial ossification, for in the rat ossification takes place without them. Where they do occur the part they play in epiphysial ossification has already been described.

SUMMARY

The anatomy of cartilage canals as restored by reconstruction from serial sections is described in detail. The various types found before a centre of ossification appears in the epiphysis, are distinguished as:

1. *Simple canals, branched and unbranched,* which project into the cartilage and end blindly.

2. *Double and multiple rooted canals,* arising by two or more roots which join within the cartilage and thereafter behave as do the simple canals.

3. *Tunnel canals,* which pass straight through a projection of the cartilage, from one side to the other.

4. *Divided canals,* which break up into two or more branches, which then rejoin to form a single canal.

5. *Communicating canals,* which enter the cartilage from the perichondrium and end in the bone marrow of the shaft.

After the centre of ossification has appeared in the epiphysis, these canals are found:

6. *Nutrient canals,* which supply the epiphysis from the perichondrium, and

7. *Centrifugal canals,* which arise from the bony centre itself but otherwise behave as do simple canals.

These canals may be found in all large cartilages, but not in small cartilages such as the epiphyses of the rat.

The successive stages in the development of cartilage canals are described and a *theory of inclusion* advanced to account for the facts discovered. It is argued that the canals are portions of the perichondrial connective tissue, and blood vessels engulfed in the growing cartilage, rather than structures which have grown into the cartilage by solution of its matrix.

The functions of cartilage canals and the effects of their presence, deduced from the anatomical data, are:

1. They carry nutriment into the interior of blocks of cartilage too large to be supplied by diffusion through their substance, thereby allowing the cartilage to grow, and preventing early calcification or death. This is the primary function, other effects being secondary or incidental.

2. They are responsible for new cartilage cells being added to the epiphysis.

3. They determine when present the position of the centre of ossification within the cartilage. They provide the tissues for the formation of both the bone and the marrow of the epiphysial centre. They carry a blood supply to the epiphysial centre while it is still surrounded by cartilage.

My thanks are due to Prof. M. R. Drennan and to Prof. R. A. Dart for the interest they have taken in this investigation, and to the Research Grant Board of the University of Cape Town for defraying expenses.

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M. RETRACTOR BULBI (OCULI) IN CARNIVORA AND UNGULATA

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EXPERIENCE has shown that statements in the current text-books relating to the retractor muscle of the eyeball of the domestic Ungulates are not entirely consistent with facts. Ellenberger and Baum (1), for example, in their description of the ocular apparatus of domestic Mammals in general, assert that the muscle "endet mit 4 Zacken dicht hinter dem Äquator des Bulbus an der Sclera. Man kann ihn (besonders bei den Fleischfressern) in 4, dem 4 Mm. recti bulbi entsprechende Abteilungen zerlegen...." And Sisson (2), referring to the muscle in the horse, states that it "is incompletely divided into four parts which alternate with the recti."

The disposition of the muscle in the dog and cat, on the other hand, has been correctly described by a number of writers. In 1907, R. du Bois-Reymond (3), in a note on the innervation of the retractor, said: "Der sogenannte 'Retractor bulbi' ist, wenigstens bei Hund, Katze und Kaninchen, nicht, wie sein Name besagt, ein einheitlicher Muskel, sondern er besteht aus vier deutlicher getrennten Muskeln, die allerdings dicht aneinander geschlossen sind. Sie entsprechen ihrer Lage nach den vier Recti." And, more recently, Reighard and Jennings (4), in their description of the anatomy of the cat, state that "the retractor oculi arises about the optic foramen and divides into four heads which lie nearer the eyeball than the recti and are therefore partly covered by the latter. They alternate with the recti and are inserted into the eyeball at about the equator, except the inferior division, which is inserted on a line with the recti."

The dissection of a considerable number of domestic dogs and cats raises no doubt that the current account of the muscle in these animals is correct, allowance always being made for occasional variations, not however greater or more frequent than are to be expected in most muscles of the body. Fig. 1 may serve as a simple scheme to illustrate the insertions of the retractor into the sclera as it occurs in the dog. It may also serve in general for the cat (fig. 2). In the scheme it has been found useful, for purposes of comparison, to indicate the four parts of the muscle numerically, beginning with the upper lateral part.

It was thought that it would not be without interest to examine the muscle in other Carnivora, and endeavour to find out if its arrangement is constant, or, if not, what are the possible variations. Up to the present only a limited number of forms have been examined; but, small though the number is, features that seem to be of moment have been disclosed.

The wild Carnivora in which the retractor has been examined are as follows: racoon (*Procyon lotor*), Japanese bear (*Ursus japonicus*), sloth bear (*Melursus labiatus*), jackal (*Canis aureus*), lion (*Felis leo*), ocelot (*Felis pardalis*), puma (*Felis concolor*), snow leopard (*Felis uncia*) and lynx (*Felis lynx*).

Of this small collection only the racoon and the sloth bear showed notable variation from the disposition of the muscle in the domestic dog and cat; but in both these animals the variation is probably of considerable significance. Fig. 3, illustrating the division of the muscle in *Ursus japonicus*, may be taken as representative, in general, of the other wild Carnivora examined.

In *Procyon lotor* the muscle is divided into two parts only, an upper and a lower (fig. 4). By chance, of the animals outside Carnivora and Ungulata, a squirrel has been examined; and in this animal the muscle was found to be divided into two parts comparable to those of the retractor of the racoon (fig. 5). It would be interesting to determine whether this simple disposition is usual among the Sciuridae; and it is tempting to consider that the racoon exhibits a primitive formation of the retractor in the series of Carnivora. Lack of material, however, forbids assertion on either point.

Melursus labiatus exhibited a variation in another direction. In both eyes the retractor divided into the orthodox four parts; but on the left side of the body there were two additional, and shorter parts (fig. 6, *5* and *6*) attached to the sclera within the regular slips of the muscle, and approximately on a horizontal level with the penetration of the sclera by the optic nerve. On the right side the more lateral of the additional parts was absent. It is perhaps justifiable to think that the absence was accidental, and that six parts in all is the regular arrangement. Certainty, of course, can only be arrived at by the examination of additional material, and this is scarcely likely to be available within a reasonable length of time.

While the Carnivores present, on the whole, a uniformity of disposition and a symmetry in the arrangement of the retractor muscle in the two eyes of the same individual, the Ungulates exhibit features of unexpected difference.

Numerous examples of all the domestic Ungulates have been specially examined, and the following wild animals have been compared with them: vicugna (*Auchenia vicugna*), reindeer (*Rangifer tarandus*), black buck (*Antilope cervicapra*), gaur (*Bos gaurus*), and buffalo (*Bos americanus*).

In every Ungulate examined the retractor formed a hollow cone, enclosing the optic nerve, with a main base of attachment just behind the equator of the eyeball. The line of attachment is not necessarily of uniform width, nor is it necessarily absolutely continuous. Interruptions may occur, or in other ways the muscle may be divided into parts. But to claim that it is divisible into four parts and to endeavour to homologise its parts with those of the muscle of Carnivora is vain. Bundles of fibres and parts of the muscle are too irregular in size and disposition to permit this to be done with even the smallest degree of satisfaction.

But a feature of the Ungulate retractor that apparently has been either

entirely overlooked or not sufficiently appreciated is the occurrence of numerous smaller bundles of fibres within the hollow cone formed by the main part of the muscle; that is, nearer to or in contact with the optic nerve, and attached to various spots on the back of the eyeball. The schemes given in figs. 7, 8 and 9 are intended to illustrate this arrangement as it has been found in *Antilope cervicapra*, *Bos gaurus* and *Bos americanus*; and may be taken, in their main features, to represent the condition in other Ungulates.

It may perhaps be permissible to consider these irregular, variable and scattered bundles as equivalent to the parts of the retractor numbered *5* and *6* in fig. 6, which schematises the insertion of the muscle in *Melursus*. There is, however, this great difference: whereas in *Melursus* definite parts of the muscle find insertion to the sclera at strictly localised places, in ungulates there are apparently few if any parts of the sclera behind the equator that may not be called upon to afford attachment for the retractor.

The best detailed description of the retractor muscle in an Ungulate with which the present writer is acquainted is that given by Sir Frederick Smith (5), who, in 1922, in this *Journal*, discussed the accessory organs of the eye of the horse. After describing the general shape of the muscle as being that of a cone containing a core of fat, Smith goes on to say that "the fibres of the muscle are loosely connected so that bundles of muscle tissue are readily seen, and fibres, some as delicate as sewing cotton, can be obtained without difficulty." From these words and from the statement that "speaking generally the muscle is inserted into the posterior half of the globe," it is evident that the diffuse insertion of the muscle had been noted. But the observer evidently could not free himself entirely from the conception that four parts of the muscle should be recognised, for he says: "The capsule of Tenon envelopes the general structure and also sends in septa, the larger of which have the effect of grouping the muscle into four quarters corresponding to the recti series." Nevertheless he clearly felt some misgiving, for, later, he adds that "it is perhaps the sinuous outline of the insertion more than anything else which indicates that it is roughly arranged in four groups."

But the most striking peculiarity of the muscle in Ungulates is its remarkable variability generally; and, further, there is good reason to think that even different individuals belonging to the same species present different patterns of insertion. To demonstrate this in the wild members of the order would necessitate the examination of a larger number of animals than is likely to be obtainable by any one person within a reasonable length of time. But to collect a sufficient amount of material from domestic Ungulates has, of course, presented no difficulty. To illustrate the variation, therefore, four pairs of equine and four pairs of bovine eyes have been taken as they came. These were dissected with all possible care, photographed, and schemes of them drawn all to the same scale (figs. 10 and 11). Eyes of the larger domestic Ungulates were chosen for this purpose because the possibility of overlooking small bundles of fibres is naturally less in them than it is when dealing with the eyes of small

animals. The result of inspection of sections of the eye muscles of the sheep and pig under the microscope was sufficient warning of the danger of error in this direction. Fig. 12, drawn under the camera lucida, shows the minute size of some of the muscle bundles in the sheep; and there can be little doubt that many of these would have escaped detection had the muscle been subjected to ordinary naked-eye dissection.

There is a further peculiarity to which attention should be directed. So far it has never been found that the pattern of insertion is precisely the same in the two eyes of the same individual. Some degree of difference has always been found, and sometimes the difference is considerable.

Allowing for the possibility that, even in the larger animals, microscopic bundles may be overlooked, there seems to be sufficient evidence to make it safe to say that there is no precise pattern common to individual members of the same species, and little approach to exact symmetry of disposition in the two eyes of the same individual.

From the observations recorded in the foregoing paragraphs, the following conclusions appear to be justified:

(1) In the majority of Carnivora the retractor muscle of the eyeball is divided into four parts, which alternate in position with the recti and are attached to the sclera behind the insertion of these muscles. This is in accordance with the current descriptions as applied to the dog and cat.

(2) Exceptions to the usual arrangement have been found in *Procyon lotor*, in which there were two parts only, and in *Melursus labiatus*, where six parts were found. In *Melursus* the two extra parts were attached to the sclera behind the insertions of the four parts customarily present in Carnivora.

If two exceptions to the rule have been found in only nine representatives of Carnivora it seems reasonable to suspect that others would be discovered if the whole order were reviewed.

(3) In Ungulata there is an irregularly (and, frequently, interrupted) circular attachment of the main mass of the muscle close to the equator of the eyeball, and a variable number of bundles of fibres of varying size inserted nearer the optic nerve.

(4) In Ungulata the pattern of insertion of the retractor is not necessarily the same in different members of the same species, nor the same in the two eyes of the same individual.

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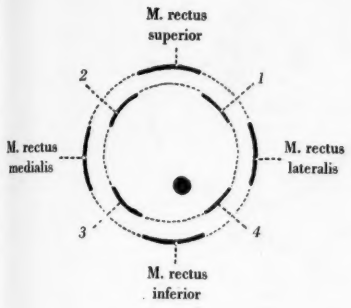


Fig. 1.

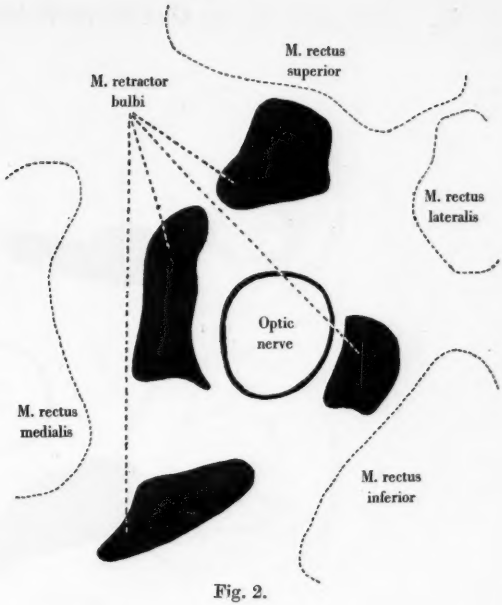


Fig. 2.

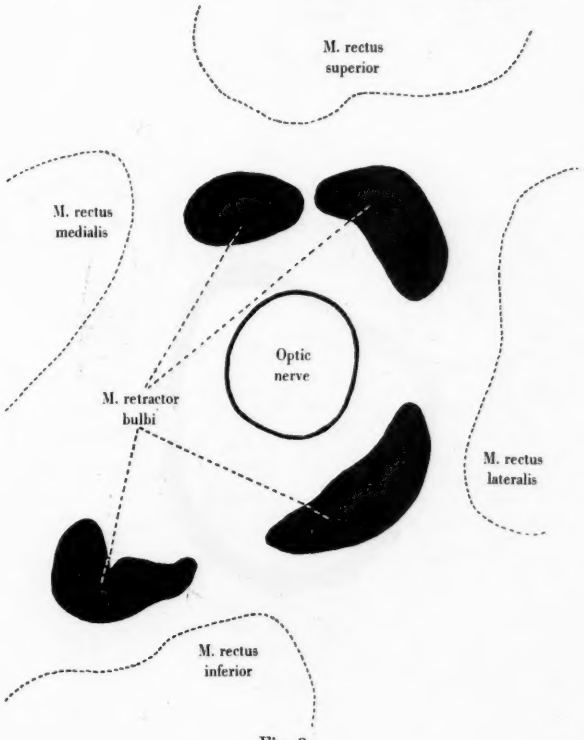
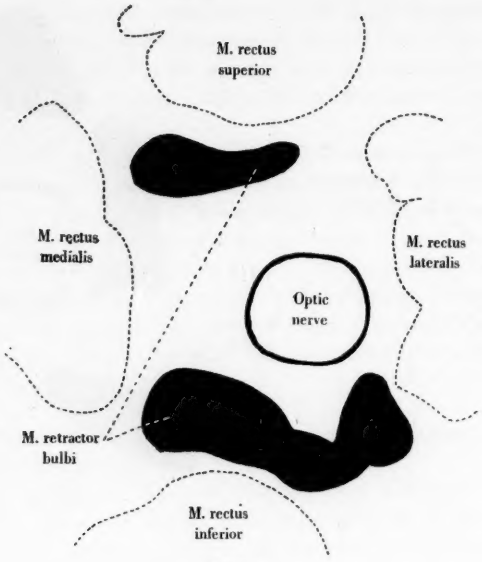


Fig. 3.


M. rectus
superior
M. rectus
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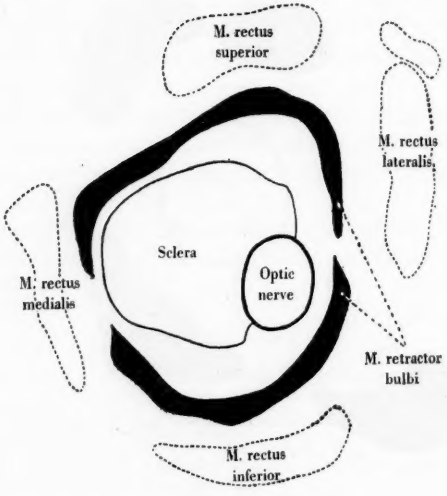
M. rectus
lateralis
Optic
nerve
M. retractor
bulbi
M. rectus
inferior

Fig. 4.


M. rectus
superior
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M. rectus
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Fig. 5.

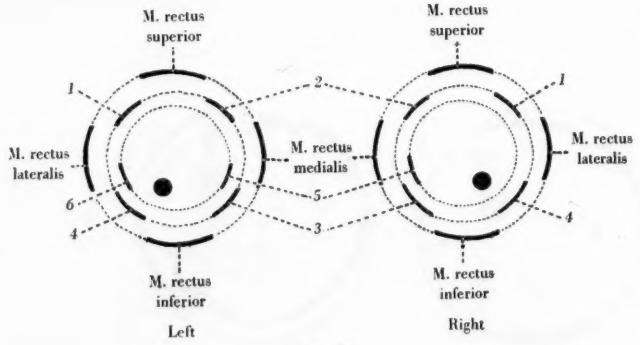
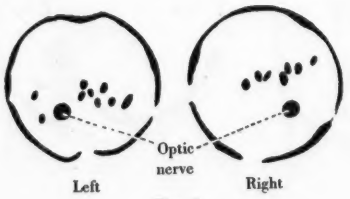


Fig. 6.



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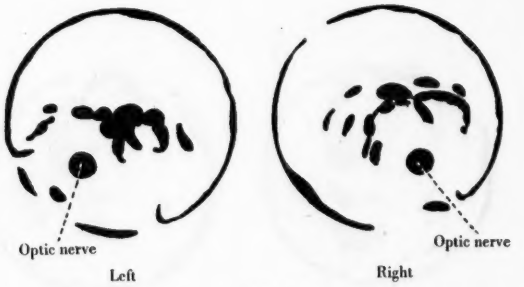


Fig. 8.

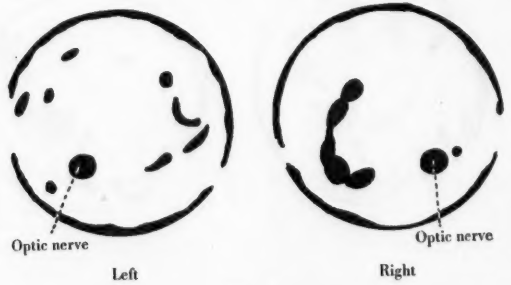
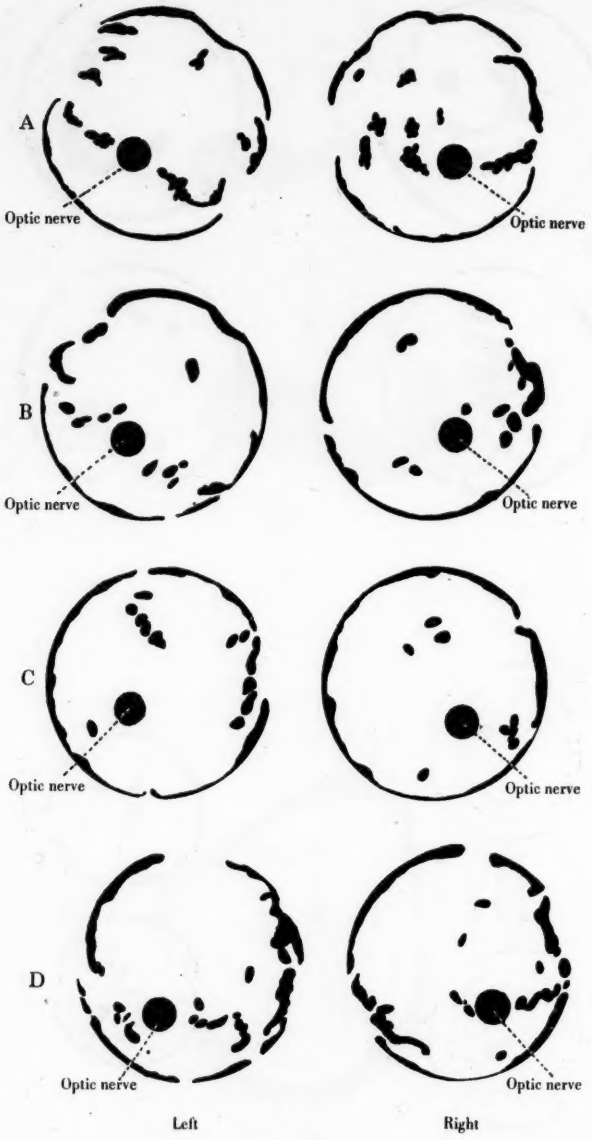


Fig. 9.


A
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C
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D
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Fig. 10.

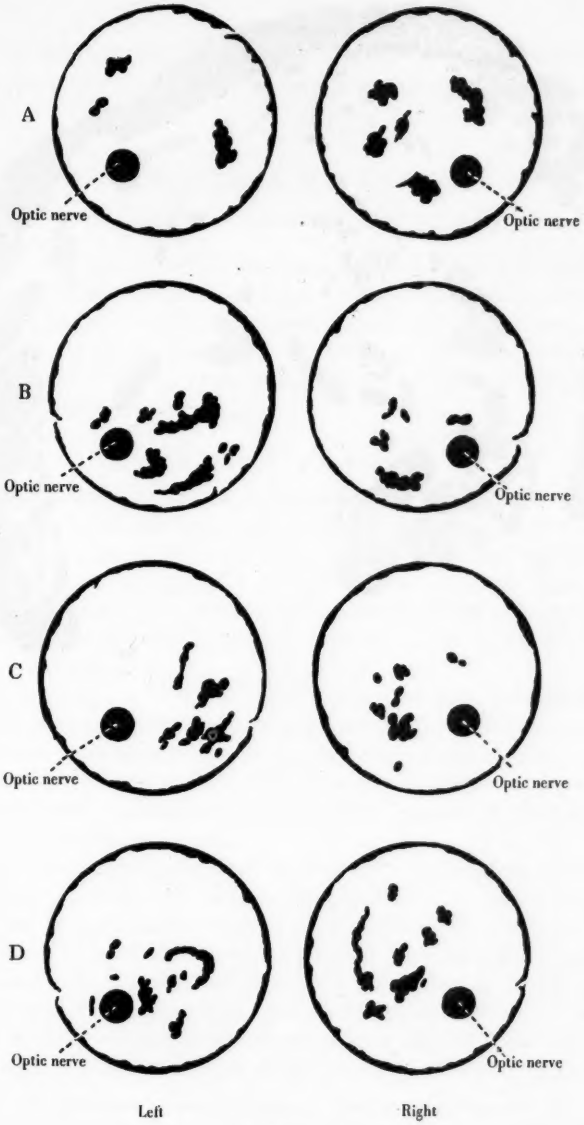
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Fig. 11.

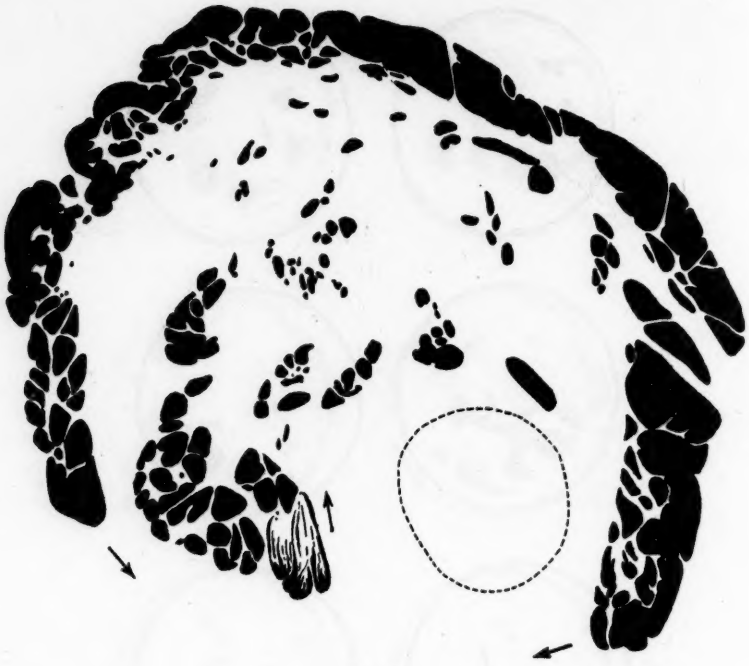

Fig. 12.

NOTES ON IRREGULARITIES OF OVOGENESIS AND ABNORMAL DEVELOPMENT OF THE EMBRYO IN *CAVIA*

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The purpose of this paper is to put upon record instances of irregularities in ovogenesis and of deviations from the normal in the early stages in the development of the embryo of *Cavia*. These specimens were obtained during a series of investigations on the development of *Cavia* with particular reference to the appearances in the ovaries and the changes undergone by the uterus in pregnant and non-pregnant animals.

A. PLURIOVULAR FOLLICLES

The widespread distribution of the pluriovular follicle in Mammalia is well known, but, as Mainland (1928) points out, the frequency with which ovaries containing pluriovular follicles are met in a series of ovaries has been worked out in some animals only, such as cat, dog, *Dasyurus viverrinus*, Texas armadillo, opossum, pig, mouse and by himself in the ferret[1]. In the mouse, Engle (1927) records polyovular follicles in twelve ovaries in a series of one hundred taken from sixty-four animals.

In the course of a study of serial sections of both ovaries of fifty-two guinea-pigs, with special reference to the corpus luteum and ovogenesis, pluriovular follicles were observed by me in only three animals. This fact seemed worthy of record as giving some indication of the comparative rarity of the condition in *Cavia*, and from the circumstance that one of these animals was pregnant and its history known.

The pregnant animal previously littered two. It was then placed with the male and killed 19 days afterwards. One normal embryo was found in each uterine horn. Both ovaries cut serially showed pluriovular follicles. In ovary A ten pluriovular follicles were observed of which one was relatively large, three medium-sized and six small, and all were at the surface of the ovary[2]. One of the small follicles contained three ova, but all the others only two. These follicles were so orientated in the ovary that in nine of them one ovum was placed peripherally and the other at the central pole of the follicle. In some,

[1] Reference may be made to Mainland's paper (1928) for the literature on this subject.

[2] Normal mature follicles according to Evans and Swezy (1931) vary in size between 900 and 1260 microns. The relatively large follicles of the above description measure from 650 to 750 microns in diameter, the medium-sized from 450 to 550 microns, and the small from 170 to 250 microns.

one ovum was the smaller and usually that nearer the surface. In the smaller follicles there was no follicular cavity, and the ova lay surrounded by granulosa cells, though in the medium-sized follicles, and single large follicle, a follicular cavity with liquor folliculi was present. Some of the smaller ova appeared normal, and in the medium-sized follicles one ovum usually showed degenerative changes. The large follicle was atretic with the two ova lying free in its cavity and surrounded by a few follicular cells.

Six pluriovular follicles were observed in ovary B of the pregnant animal, and all at the surface of the ovary. One of these was relatively large, measuring 678 microns in diameter, and contained two ova each in a separate cumulus and widely separated by a large follicular cavity containing liquor folliculi. The ovum nearest the surface was smaller, showed evidence of degenerative changes and was covered with a single layer of granulosa cells. The larger ovum was apparently healthy and situated at the central pole of the follicle, being covered by several rows of granulosa cells. Deep to the larger ovum in the most central part of this large follicle was a second smaller cavity containing liquor folliculi. The entire follicle was surrounded by a well-marked tunica externa and interna. The other five pluriovular follicles in ovary B were small; four of these were biovular, but the fifth had four ova of which two showed degeneration. Some showed a small follicular cavity, others did not, and the ova in the smallest follicles appeared healthy. From the history of this animal the presence of pluriovular follicles would seem to bear no relation to fertility. In this connection it may be noted that Hartman (1926) recorded the presence of numerous pluriovular follicles in two pregnant macaques, and neither had twin embryos.

In one non-pregnant animal two largish biovular follicles and several smaller ones were found in each ovary, and the former as well as some of the latter showed degenerative changes. The ovaries of the other non-pregnant animal showed much the same appearances.

Loeb (1901) occasionally found follicles with two ova in the guinea-pig, and in some of these the ova were unequal in size. Disparity in size of the ova in a pluriovular follicle is apparently fairly common in other animals. Hartman (1926) states that the explanation probably lies in the differential growth potentialities of the eggs and different thresholds of response to growth stimuli, and points out that since normally many primordial ova remain quiescent, whereas others enter the growth period, it is to be expected that if a number of ova are fortuitously united into a single follicle, they will nevertheless exhibit their individual properties and either grow or remain retarded, as the case may be. On the other hand, Loeb (1917) has described pluriovular follicles of the guinea-pig in which primordial follicles "push their way into larger follicles, perhaps into such follicles which are already in the process of degeneration," and in favour of this interpretation he mentioned that in the majority of cases the more undeveloped egg is situated toward the outer pole of the follicle. Mainland (1928) states that degeneration seems to be the usual fate of

these follicles, and in this connection it may be noted that most of those recorded here showed some evidence of degeneration.

Various theories have also been suggested to explain the occurrence of such follicles. There does not appear to be much evidence to support their origin from polynuclear ova, and no example of the latter was encountered by me. Loeb (1917) found numerous pluriovular follicles in what he calls the "hypotypical" ovaries of a guinea-pig which had been used in "under-feeding" experiments, and had its thyroid removed and the lobe of another thyroid engrafted subcutaneously. He claims that in this animal there was manifested a relative decrease in the amount of the connective tissue surrounding the follicles, and suggests that pluriovular follicles may be formed by a concrescence of previously separate follicles.

A lack of balance in development between the follicular tissue and the connective tissue, at the stage in the embryonic ovary when the small follicles normally become separated from each other, is the explanation favoured by O'Donoghue, Hartman, Mainland and others. In support of this I have observed several examples in which the connective tissue formed a definite layer around two small ova, yet there was at this stage little if any attempt to penetrate between them. What would normally have resulted in these instances cannot be foretold, but it seems reasonable that if the connective tissue failed to separate the ova that a biovular follicle would result. Evans and Swezy (1931) maintain that in the Mammalia all the ova of adult life are new formations, and state that the common method of formation of new ova in the guinea-pig is for a group of cells to be pushed inward from the germinal epithelium, usually as a solid cord which soon becomes cut off from the epithelium and comes to lie along the inner border of the tunica albuginea. One or more cells in each group then become enlarged to form the ova, and the remaining cells form the follicle cells; occasionally most of the cells in a group change into ova forming polyovular follicles, but these soon disappear, as large follicles containing more than one ovum are relatively rare in the guinea-pig.

The occurrence of pluriovular follicles in *Cavia* is apparently uncommon. It may be, however, that the condition is not quite as rare as would appear from the present series of ovaries, since the examination of the latter was carried out chiefly with reference to the corpus luteum and the appearances of medium-sized and large follicles, and perhaps occasional small pluriovular follicles may have been overlooked.

B. ABNORMAL EARLY DEVELOPMENT OF THE EMBRYO

There are few records of abnormalities in the early stages of Rodents, and so far as I am aware, none such as are here described have been recorded in *Cavia*. Abnormal ova in different groups of Mammals have been recorded by various writers, including Huber (1915) in the rat, Hill (1910) in *Dasyurus*, Hartman (1919) in the opossum, Corner (1921) in the pig, Robinson (1921) in the ferret, Sobotta (1924) in the mouse, and Hammond (1914) in the sow and

rabbit. Meyer (1917) has recorded several examples of degenerate guinea-pig embryos in pregnant animals from 19 to 37 days after coitus, and Squier (1932), dealing with the living guinea-pig egg and its early development, has described pathological morulae, four-celled stages, and blastocysts. My specimens are described not so much in the interest of comparative or experimental teratology, but as giving some interesting sidelights on the peculiar and specialised early stages seen in *Cavia*.

Abnormal or retarded segmentation

The first preparation (Plate I, fig. 1) shows the appearance of an abnormal segmented ovum. The specimen was found at the midpoint of uterine horn A of *Cavia* No. 64 at the anti-mesometric side of the lumen. Another abnormal segmented ovum was found in horn B of the same animal and almost identically placed. The ovum (Plate I, fig. 1) appears to consist of eight cells, maximum possible age 138 hours, and measures, including zona, 0·07 × 0·039 × 0·07 mm. The zona has partially degenerated and the normal development of the ovum seems to have been arrested. The nuclei are still apparently healthy and the cell protoplasm finely and fairly evenly granular. Plate I, fig. 2, represents a normal eight-cell stage. The ovum, including zona, measures 0·066 × 0·043 × 0·08 mm., maximum possible age 72 hours, and is still in the tube. The well-developed zona and the appearance of the cytoplasm in the normal specimen, due to the distribution of the lipoid globules represented in the figure by rounded spaces, distinguish it from the abnormal ovum (Plate I, fig. 1).

It will be noted that the normal eight-cell stage and this abnormal eight-cell stage compare closely in measurement, and that while the former is still in the oviduct the latter is half-way along the uterine horn. A normal sixteen-cell stage, maximum possible age 106 hours, and measuring about 0·119 mm. in diameter, is still in the tube near the tubo-uterine junction. Such abnormal ova may occur with normal ova in the same uterus. The possibility is, however, always to be guarded against that such structures may not be of ovarian origin, but belong to the category of "false embryos," i.e. decidual remains. The uterine epithelium and the endometrium in both horns of *Cavia* No. 64 appeared healthy.

Young abnormal segmenting eggs such as the one figured, or the fragments of them, and ova which have either not been fertilised or have failed to develop, were not of infrequent occurrence, but a numerical record of them has not been kept. Such abnormal ova have also been found in the rat (Huber, 1915) and in the mouse (Sobotta, 1924).

Abnormal blastocyst formation

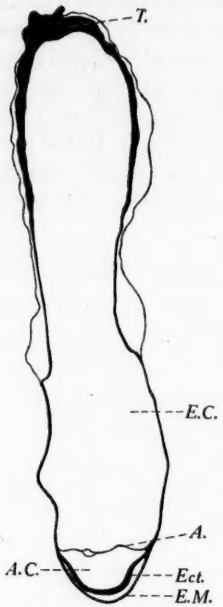
The example of this type shown (Plate I, fig. 3) is one of two "blastocysts," both abnormal, which were observed at the tubo-uterine junction of horn B of *Cavia* No. 33. No ova were found in the other tube or horn. Each presents very similar appearances, measuring 0·06 × 0·038 × 0·06 mm. including zona,

and maximum possible age is 4 days. Plate I, fig. 3, represents a median section through one of these abnormal ova and shows a well-marked zona enclosing a degenerated cellular mass, the nuclei of the cells having practically all disappeared. Plate I, fig. 4, shows for comparison a normal blastocyst of maximum possible age 5 days, measuring, including zona, 0·072 × 0·045 × 0·05 mm., and nestling against the wall of a pocket on the anti-mesometric side of the uterine horn. This blastocyst is cut in approximately the same plane as the abnormal one. In contrast to the abnormal example which is about the same size as this normal blastocyst, the cells of the latter are fewer and the nuclei large and prominent. Abnormal ova such as is shown (Plate I, fig. 3) have frequently been found by workers in this Department, some along with normal blastocysts in the same uterus, and in all examples it was noted that the tubes and uterine horns appeared healthy and normal. Huber (1915) has described abnormal segmentation cavity formation in ova obtained from the uterus of the rat, and Corner (1921) has recorded degenerate blastocysts in the pig.

Suppression of the trophoblast

The third specimen to which attention is drawn was obtained from the uterus of *Cavia* No. 77. In horn A was found a normal embryo (text-fig. 1), of maximum possible age 13 days, and at the stage when the amnion cavity is well developed and its roof double-layered, the mesoderm having appeared in a normal manner. In horn B the rudiment shown in Plate II, fig. 6, was encountered and is probably about the same age. It was found in a swelling almost similar in size to that which contained the normal embryo in the other uterine horn, and occupied a very small decidual cavity (Plate II, fig. 5) confined to the extreme mesometric side of the uterus. The structure is very small, measures 0·1 × 0·1 × 0·1 mm., and consists (Plate II, fig. 6) of a small cavity with a thin single-layered roof and elsewhere a double-layered wall; the latter is better appreciated in the stained sections of the actual specimen as owing to a slight obliquity only some of the nuclei are showing in both rows in the same section. The thin roof in the fixed specimen is directed towards the mesometric side of the uterus, and though it must be admitted that the rudiment may have rotated in the process of preparation this seems unlikely. The interpretation of the specimen is difficult and must be only conjectural, yet the appearances are perhaps sufficiently interesting to warrant some suggestion as to what they might represent. I regard the cavity as that of the amnion roofed mesometrically by thin amniotic ectoderm and lined elsewhere by embryonic ectoderm, the outer layer of cells adhering to the latter being probably formative endoderm, the remainder of the embryo having been suppressed or failed to develop. There is no evidence of träger or mesoderm or any embryonic fragments. It will be noted that the specimen occupies a very small decidual cavity at the extreme mesometric side of the uterine lumen, and the view might be advanced that it had become embedded here instead of as normally at the anti-meso-

metric side of the lumen, and that this faulty implanation may in some measure have contributed to its failure to develop normally. In this connection it may be noted that "implantations" on the mesometric side of the uterine lumen in the guinea-pig, as illustrated by Emrys-Roberts (1910), appear to belong to the class of "false embryos" described by Maclaren (1926). The endometrium of the uterus was healthy and normal. In the pig Corner has recorded a very interesting abnormality consisting of total absence of an embryonic area.



Text-fig. 1. Diagrammatic drawing of normal embryo No. 77 of maximum possible age 13 days. × *circa* 18.

A. amnion, showing ectodermic and mesodermic layers; *A.C*. amniotic cavity; *E.C*. extra-embryonic coelom; *Ect*. ectoderm; *E.M*. endoderm plus mesoderm; *T*. träger.

Abnormal uterine swellings and arrest of development of the embryo

It is well known that in the mouse, rat, ferret and other Mammals, there are fairly commonly found uterine swellings which, when sectioned, contain only fragments of an embryo. These swellings may be almost as large as those containing a normal embryo of the same age, but are usually somewhat smaller. Such abnormal swellings are also encountered in *Cavia*, though compared with the number of uteri examined in this Department they appear relatively uncommon. In some cases the swelling is practically uniformly solid and only by most careful serial examination can embryonic fragments be discovered; in other cases the decidual cavity or parts of it can be recognised.

Sometimes the swelling contains an embryo arrested in its development. This does not appear to be common. The uterus of *Cavia* No. 18 contained four embryos of maximum possible age 14 days, all in the same uterine horn. The embryonic swellings were about equal in size. Two of the embryos were normal, the other two showed what appeared to be arrested development, and all four were sectioned in approximately the same axis. The normal embryos are at the stage of development of that shown in text-fig. 1, and each measures by sections 0·96 mm. Plate II, fig. 7, illustrates the first of these abnormal embryos. It measures 0·55 × 0·23 × 0·4 mm., and is therefore much smaller than the normal of this age. The specimen shows an abnormal träger, continuous with which is a degenerating amnio-embryonal cell mass covered by degenerating endoderm. The proexocoelomic cavity is absent and the apparent central opening is proved by serial examination to be a crack. The specimen is attached by its träger end to the extreme mesometric side of the uterus and occupies a fairly extensive decidual cavity. This seems to have been a normal implantation at the anti-mesometric side of the lumen, but development of the embryo has been early arrested and the specimen has reached its present position by differential growth. The endometrium appeared to be normal and healthy.

The second abnormal embryo found in the uterus of *Cavia* No. 18 measures by sections 0·79 mm. and the formative end 0·28 × 0·195 × 0·24 mm. It is therefore much smaller than the normal embryo found in this uterus though its decidual cavity is as large, and implantation seems to have been normal. Embryos from the same female may differ slightly in their stage of development but not so markedly as in this case (cf. text-fig. 1 of normal embryo). Plate II, fig. 8, is a somewhat diagrammatic drawing of a median section of the formative end of this abnormal embryo. There is considerable development of mesoderm, but the amnio-embryonal ectodermal cells show appearances which seem to deviate from the normal. The amnion cavity has appeared, but the cells surrounding it are very numerous and appear to be breaking up into numerous smaller cells showing evidence of degeneration. The specimen would not permit of a photograph good enough for reproduction, but the drawing (Plate II, fig. 8) gives some impression of the great number of amnio-embryonal ectodermic cells. The decidua seems healthy and the träger normal, though smaller than that of the normal embryo found in this uterus (text-fig. 1). The abnormal appearances of this formative end are better appreciated when compared with the formative end of a normal embryo which has reached approximately the same stage of development (Plate III, fig. 9), and is of maximum possible age 15 days. The developing amnion cavity in this normal embryo is seen as a slit in the median line of the formative knob with the cells of the formative ectoderm arranged more or less radially to the axis of the slit. No such arrangement can be seen in the abnormal specimen (Plate II, fig. 8), and moreover in the latter case neither the cells nor their nuclei are so large and healthy as in the normal specimen. The general appearance of the specimen suggests that the amnio-embryonal ectoderm was in incipient disintegration

some time before the specimen was fixed, i.e. normal development had been arrested.

It may be of interest to note that Huber (1915) has recorded two examples of rat egg-cylinders in which the only abnormality observed is in the region of the ectodermal node. These cases he interprets as showing a retardation of the development of the ectodermal node and differentiation of the primary embryonic ectoderm.

Two embryos in a single decidual cavity

This interesting specimen (Plate III, fig. 10) must represent an exceedingly rare condition. It shows two embryos of maximum possible age 14 days enclosed within a single decidual cavity. The upper embryo is the smaller, its mesoderm has not yet appeared, and it represents a younger stage of development than the lower older and larger embryo which shows considerable development of mesoderm. Serial examination proves each embryo to be complete, there being no connection between the träger ends which are normally directed towards the mesometrial side of the uterus. The condition described above bears a close resemblance to the very rare case of two egg-cylinders in one decidual crypt described by Huber in the rat. In Huber's fig. 10, p. 137, the two egg-cylinders have in part a common ectoplacental cone, but he states that the ectoplacental cones are for a short distance distinct before partial fusion occurs, showing that each egg-cylinder developed from a separate ovum. As in the present case the upper egg-cylinder represents a younger stage of development in which no mesoderm is present, while the lower and larger one is at a later stage and shows considerable mesodermic development. Huber believed that both ova were seminated at about the same time, became lodged in close proximity in the same uterine mucosal fold, and with further development of the decidual crypts both became enclosed within the same crypt at perhaps slightly different levels. In further development one blastodermic vesicle developing more rapidly dominated the other. The appearances he believes are not to be explained on the supposition of superfecundation or superfoetation. He also gives evidence to support the view that when two morula masses are lodged in close proximity in the same mucosal fold one or the other degenerates, and that the normal development of both is of very rare occurrence. In the oviducts in *Cavia* several examples have been observed where two apparently normal segmenting ova are adherent to one another, and it may be suggested that this case of twin embryos resulted from two such ova which had remained adherent and become implanted together, one later growing more rapidly at the expense of the other.

These examples of abnormal early development in *Cavia* may be grouped into Huber's two main classes, first, those in which all the ova of a given animal show abnormal development, and second, those in which an abnormal ovum is found in the same uterus along with an average number of normally developed ova. As I have already said I do not propose to discuss these cases from the

point of view of comparative or experimental teratology. Nor shall I deal with the theories respecting the underlying cause of the departures from normality which have been classified and discussed by Corner (1923), but it may be noted that in each case the maternal structures were examined with care and seemed to be anatomically and functionally normal. I am unable to report on the ovaries since they were unfortunately not preserved.

It seems, however, that in this series the abnormalities were not due to local maternal conditions, but represent some embryonic imperfection. Stockard, from experimental results, maintains that changes in the condition of moisture, temperature and oxygen supply are the most frequent causes of embryonic death as well as monstrous development, but careful consideration of this in relation to the animal stock in this Department lends no support to the view that such conditions have been active in the production of such abnormalities as are described. Professor Robinson in his Struthers Lecture showed that a considerable amount of prenatal death is normal in Mammals. From the tables given by Stockard and Papanicolaou (1918), in the record of their experiments on the modification of the germ cells in Mammals, Robinson states that in guinea-pigs it appears that the prenatal death-rate of normal non-inbred lines is 13·30 per cent., but he regards this as rather low for *Cavia*. The ultimate fate of these abnormal embryos is merely a matter of conjecture. Meyer, describing degenerate guinea-pig embryos belonging to later phases than are dealt with in this paper, states that intra-uterine absorption is not a rare occurrence.

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EXPLANATION OF PLATES

PLATE I

Fig. 1. Section of abnormal segmented egg or egg that has failed to develop (64 A)[1] lying in the uterus. Fixed Zenker. Stained iron-haematoxylin. Photomicrograph. × *circa* 500. Compare fig. 2.

Fig. 2. Section of normal eight-cell stage (34 A) in the oviduct. Fixed Zenker. Stained iron-haematoxylin. Photomicrograph. × *circa* 500.

Fig. 3. Section of abnormal blastocyst (33 B). Fixed Zenker. Stained haemalum and eosin. Photomicrograph. × *circa* 660. Compare fig. 4.

Fig. 4. Section of normal blastocyst (24 A) lying in the uterus. × *circa* 570. From Maclaren (1926).

PLATE II

Fig. 5. Section of embryonic rudiment (77 B) in small decidual cavity. Fixed Zenker. Stained iron-haematoxylin. Photomicrograph. × *circa* 120.

Fig. 6. Same as fig. 5. × *circa* 425.

Fig. 7. Section of embryonic rudiment (18 B). Fixed Zenker. Stained haemalum and eosin. Photomicrograph. × *circa* 108.

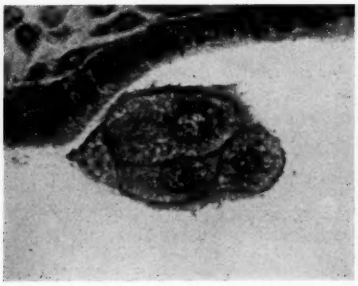
Fig. 8. Diagrammatical drawing of formative knob of embryo (18 C), of maximum possible age 14 days, arrested in its development. × *circa* 150. *Am.* amniotic cavity, *E.* ectoderm, *E.C.* extraembryonic coelom, *En.* endoderm, *M.* Mesoderm. The stippling of the ectoderm of the knob gives a good impression of the breaking down of the cells into numerous nucleated masses. Compare fig. 9.

PLATE III

Fig. 9. Drawing of section of formative knob of a normal embryo (16 C) of maximum age 15 days. × *circa* 219. Explanations as in fig. 8. (From an unpublished figure—Maclaren.)

Fig. 10. Section showing two embryos (82 A) in a single decidual crypt. Maximum possible age 14 days. Fixation formalin and corrosive sublimate. Stained iron-haematoxylin. Photomicrograph. × *circa* 30.

[1] Catalogue number of parent animal.



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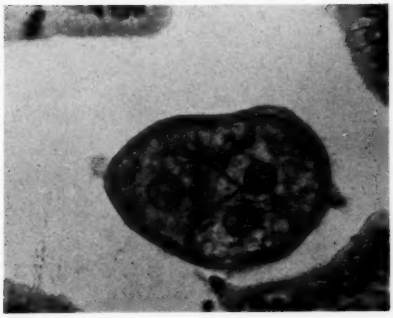

Fig. 2.

Fig. 3.

Fig. 4.

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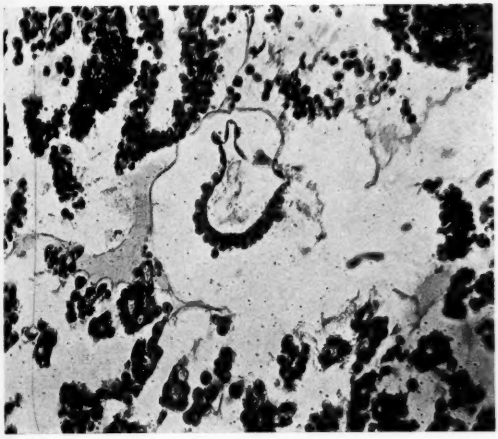
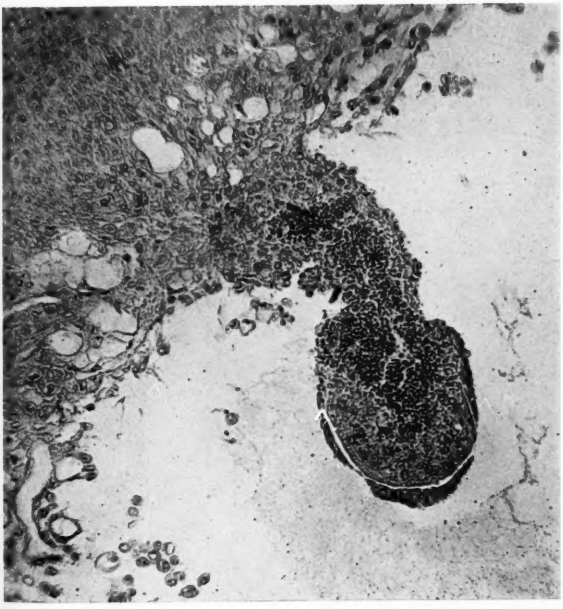


Fig. 5.

Fig. 6.



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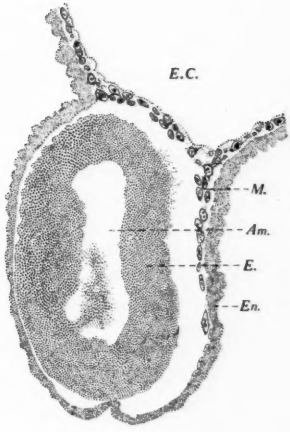

Fig. 8.

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Fig. 9.

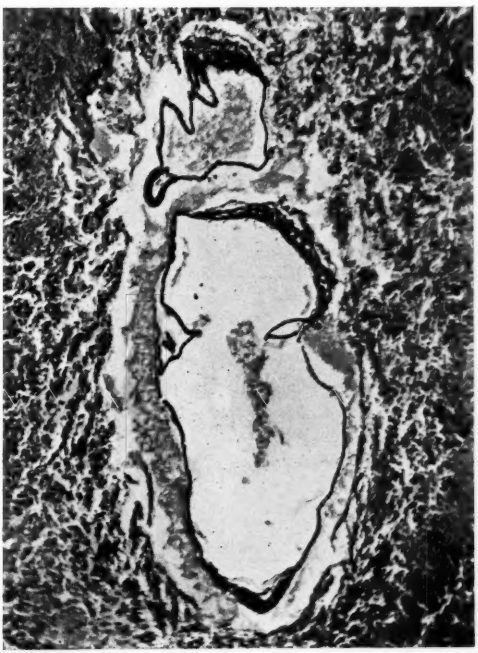

Fig. 10.

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ON SOME EFFECTS OF X-RAYS ON THE DEVELOPING CHICK EMBRYO

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In two earlier contributions to this *Journal*, the present authors in collaboration with C. P. G. Wakeley (5,6) described some of the actions of X-rays upon the development of chick embryos. Those papers dealt with the action of repeated doses, which individually were of the order of those used in ordinary superficial therapy. The present communication has reference to the effect of a single massive dose administered after incubation had proceeded normally for 9 days. In each case four full pastille doses (P.D.) were given.

An ordinary therapeutic induction coil was used: K.V. 120, M.A. 2·5, 20 cm. distance. The eggs were removed from the incubator in boxes lined with cotton-wool, and the very thin layer of cotton-wool covering them was allowed to remain during irradiation.

Dosage was estimated by the Sabouraud pastille, a method which has been shown by Owen and Bowes (16) to give fairly accurate readings within our experimental limits. No account has been taken of screenage due to the egg-shell, nor of the effects of the secondary radiations given off by the calcium contained therein. All the eggs were irradiated under the same conditions, and all belonged to the same breed of fowl. It is only fair to recognise, nevertheless, that secondary rays from calcium may play a very important part in biological experiments in which they are concerned. This fact has long been recognised, in connection with the radio-necrosis of bone, and Mottram (15) has shown that it also holds good for soft structures adjacent to bone when both are included in the same field of radiation.

If attempts are made to eliminate this source of complication in experiments, by cutting a window in the shell, we are still faced with difficulties in the production of possible artefacts due to trauma and microbial infection. Goulston and Mottram (14) have shown that error from this source is by no means negligible, and indeed may lead to entirely fallacious conclusions.

The eggs were incubated for 9 days, and were in two series according as filtration of the rays was, or was not, employed.

Screened specimens

4 P.D.	Filter 4 mm. aluminium.	Killed at once	
,,	,,	,,	Killed after 2 hours
,,	,,	,,	,, 4 ,,
,,	,,	,,	,, 6 ,,
,,	,,	,,	,, 24 ,,

Unscreened specimens

4 P.D.	No filter.	Killed at once	
,,	,,	Killed after 2 hours	
,,	,,	,,	4 ,,
,,	,,	,,	6 ,,
,,	,,	,,	24 (dead)

After exposure, the eggs which were not to be opened at once, were returned to the incubator for the requisite times. Sagittal sections were made from each embryo in the mid-axial line, and also laterally so as to include the optic vesicle and the genital ridge. All the embryos were found to be alive with the exception of one unscreened specimen in which the egg was opened 24 hours after exposure.

Fixation was effected in a mixture of potassium bichromate, 3 gm., glacial acetic acid, 5 c.c., distilled water, 100 c.c., for 24–48 hours. Specimens were washed in distilled water; transferred to 50 per cent. alcohol; then dehydrated, embedded in paraffin, sectioned and stained with iron-haematoxylin and eosin; van Gieson; or picro-indigo carmine. Details of cell structure were carefully examined throughout the series with a $\frac{1}{12}$ in. immersion lens.

GENERAL CHANGES PRODUCED BY RADIATION

The changes observed were all destructive in character; the longer the time the embryo was allowed to survive after exposure, the more marked were the changes. With the same dosage the amount of damage was diminished by increased screenage. The general effects were perhaps not so marked as might have been expected: this is probably due to the fact that the longest period of survival (24 hours, screened; 6 hours, unscreened) was insufficient to allow the full effect of radiation to be manifested. The most obvious changes were: a general blurring of the details of cell structure, the cell body appearing granular, and the distinction between cytoreticulum and cytoplasm being ill-defined or completely obscured; defective staining of the cytoplasm with eosin; detachment of epithelium; want of definition and irregularity of cell outline; and a tendency towards fusion of cells and the formation of syncytial masses.

There was frequently thickening and irregularity of the nuclear membrane and a tendency towards pycnosis.

Mitoses were *absent in two specimens, each of which had been allowed to survive for a period of 2 hours after exposure to the X-rays.* In one of these specimens a 4 mm. aluminium filter was used; the other was unscreened. In specimens killed immediately after exposure, or allowed to survive for 4, 6 or 24 hours,

mitoses were abundant; but the individual chromosomes were often irregular in disposition and clumped together in masses.

The red blood corpuscles were often markedly distorted and in some cases fragmented. The capillaries, especially those of the sub-epidermal mesenchyme and central nervous system, were frequently dilated. Those in the subcutaneous tissue were usually full of blood, indicating an incipient stasis: those in the central nervous system were generally empty or contained only very few blood corpuscles.

EMBRYONIC MEMBRANES

The embryos were removed entire with portions of the membranes attached. These included parts of the yolk-sac, allantois, amnion and chorion. The effects of radiation were difficult to assess, since these structures normally show both proliferative and degenerative changes: the former might easily be mistaken

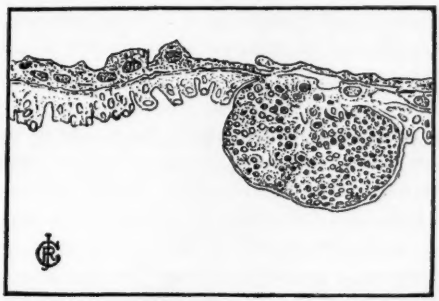

Fig. 1. Nodule of proliferating cells which projected from the inner surface of the amnion, of a normal chick embryo, incubated 9 days.

for hyperplasia or hypertrophy, and the latter for atrophy, resulting from radiation, whereas in fact both conditions occur in perfectly normal specimens.

In the experimental series, especially in the unscreened series allowed to survive for some time after exposure, the entodermal cells lining the yolk sac were extensively broken down and were irregular in form with large vacuoles. The nuclei, poorly stained, were in many cases liberated by the disruption of the cell bodies and lay free in the cavity of the sac. The mesoderm was less affected than the entoderm, but its fibres were swollen and ill-defined. Many large capillaries and sinusoidal spaces were present; these contained red blood corpuscles in different stages of development and degeneration, many being distorted and fragmented while others were devoid of a nucleus.

The epithelial cells and connective tissue of the yolk sac were in general less deeply stained than the corresponding tissues of the other three membranes. The ectodermal cells lining the amnion were often swollen and their outlines irregular and ill-defined. Localised masses of proliferating cells were occasionally observed, and such masses were also seen in the control specimens (fig. 1).

THE EMBRYO

Ectoderm

Cutaneous ectoderm. The superficial epithelial strata are frequently separated from the subjacent mesoderm. This becomes more marked with increasing exposure and diminishing filtration. In some cases there is shedding of the epitrichial layer, while the deeper layer of granular cubical cells remains. In the irradiated specimens the cell outlines are less distinct, the staining less intense and the cytoplasm more granular than in the controls. Mitoses are sometimes present, and in some specimens, allowed to survive for some time after exposure, there is dilatation of the subepidermal capillaries.

Neural ectoderm. One of the most obvious changes is a marked enlargement of the capillaries of the brain and spinal cord. For the most part these are situated at the junction of the ependymal and mantle layers. Since the spaces are almost empty and stand open, they are very conspicuous. They are present in both screened and unscreened specimens, but are most conspicuous in the latter when allowed to survive exposure for 6 hours. The cellular elements of the brain and spinal cord are not so well defined in the irradiated specimens as they are in the controls. Staining was less bright and more diffuse in the experimental series, and with the exception mentioned on p. 86 mitotic figures appeared to be equally frequent in the different categories of the experimental series and in the controls. The chromosomes were however often mis-shapen, irregularly disposed, or clumped together. Nuclei of non-dividing cells often showed irregularity of outline and thickening of the nuclear membrane, and there was a general tendency towards pycnosis.

Eye. The general picture is less clear in the irradiated specimens, and the fibres of Müller swollen and irregular. The pigment layer is uneven and folded, the pigment granules irregular and the cell outlines indefinite. The dilated capillaries and large sinusoidal spaces which were observed in the brain and spinal cord were not present in the retina, since the *pars optica retinae* at this stage is almost avascular. The capillary plexus in the mesenchyme surrounding the optic cup shows marked dilatation, with extravasation of red blood corpuscles into the extravascular spaces around the retina.

Entoderm

Examination of the epithelial lining of the respiratory and digestive tracts, and of the secretory cells of the liver and pancreas, showed general blurring of cell outlines in the irradiated specimens. In some cases the free borders of the cells were "frayed-out" with consequent escape of the cell contents into the adjacent lumen.

The cytoplasm generally showed a granular opacity, and the nuclear membranes were often thickened and irregular in shape. In the liver the endothelium lining the sinuses was not markedly affected.

Thymus. The thymus glands of chick embryos of 8–10 days' incubation are passing through a transition stage, from avascular and purely epithelial organs to the later condition in which the lobules are invaded by capillary vessels, and a reticular tissue very rich in lymphocytes is developed. The epithelial (entodermal) cells are rounded or polygonal, and the large number of mitoses indicates rapid growth. In those slightly older embryos which were allowed to survive after the exposure (e.g. a specimen 4 P.D., 4 mm. filter, killed 24 hours after exposure) penetration of vessels had advanced to a stage in which they had reached the central parts of the lobules, and a distinction between cortex and medulla was apparent. Thus the exposure to X-rays had not arrested the development and differentiation of the gland. Growth was still active as shown by the frequency of mitoses, and the organ had entered upon a new phase of development. Lymphocytes were not present in the gland itself, although in the blood vessels of the surrounding fibrous capsule there were some small spherical cells with relatively large nuclei.

Generally speaking the thymus glands of irradiated specimens showed no special features, though the ordinary cell changes—granulation of cytoplasm, thickening of nuclear membrane, etc.—were well marked. This lack of special sensitivity in the thymus of chick embryos at this stage of development is due to the low degree of differentiation attained. The adult thymus containing a reticular tissue with abundance of lymphocytes is exceedingly sensitive to radiations.

Mesoderm

Subepidermal mesenchyme. In some specimens, especially those surviving for the longer periods after irradiation, there is some dilatation of capillaries with occasional local extravasations of blood. The separation of small areas of epidermis, previously noted, sometimes corresponded to the regions in which the capillaries are dilated.

Embryonic connective tissue. The cell outlines are ill-defined and the protoplasmic strands between the cells are often torn through and irregularly retracted. Sometimes the endothelial walls of the capillaries are ruptured, and the blood extravasated into the tissue spaces.

Cartilage. Very little change could be detected in the cartilage, especially in those specimens which were killed at once. In some the matrix was more granular and the contrast between the staining of the cartilage cells and the matrix was less evident than in the controls.

Muscle. Skeletal, cardiac and unstriped muscle showed no obvious changes. In some of the specimens allowed to survive after the exposure both muscle fibres and interfibrillar substance had a finely granular appearance.

Blood (figs. 2, 3). In general the red blood corpuscles in the vessels and vascular spaces of the irradiated specimens are more granular and irregular in outline than in the control specimens. The cytoplasm is less deeply stained with eosin and the nucleus less sharply differentiated with regard to its internal

structure. A considerable number of corpuscles is distorted and in some cases they are fragmented.

The degree of staining of the nucleus with haematoxylin varies very much, some nuclei being deeply stained, while others are quite pale. Red blood-cells are sometimes seen which do not possess a nucleus and some cells have the appearance of a space from which the nucleus has been extruded, such as is occasionally seen in developing mammalian corpuscles. These are found not only in the irradiated specimens but in normal control specimens at the same stage of development.

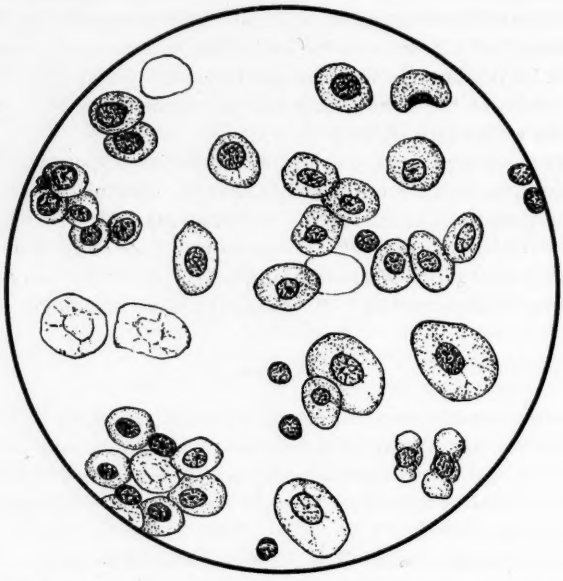

Fig. 2. Typical cells present in the blood of a 9-day chick embryo. Control specimen.

Urino-genital system

The appearance of the mesonephros is very variable. This is largely due to normal degenerative changes in the Wolffian body at this stage of development, in addition to changes produced as a result of the radiations. Consequently in assessing the effect of the radiations, only a general estimation of the differences in the degree of disintegration in the experimental and control specimens could be attempted.

The principal changes observed were: loosening of the epithelium lining the tubules with separation of the individual cells; these being frequently shed off into the lumen of the tubule. Defective staining of the cell bodies with eosin. Vacuolation of the cytoplasm. Irregularity of the free border of the cells, the edges of which were often frayed. Great variability in the appearance of the

nucleus, which was sometimes pycnotic, sometimes feebly stained and fragmented. The red blood corpuscles show every stage of degeneration and variation in the degree of staining. Some of the nuclei are pycnotic, others pale or unstained, and in some corpuscles the nucleus in absent. Haemorrhages into the intertubular spaces are frequent and there is a considerable amount of cell detritus and coagulated fibrinous material. It is probable that many of the distorted and degenerated red blood corpuscles which are found in the general circulatory system at this stage of development in both the normal and experimental series originate in the mesonephros and are swept from this organ by

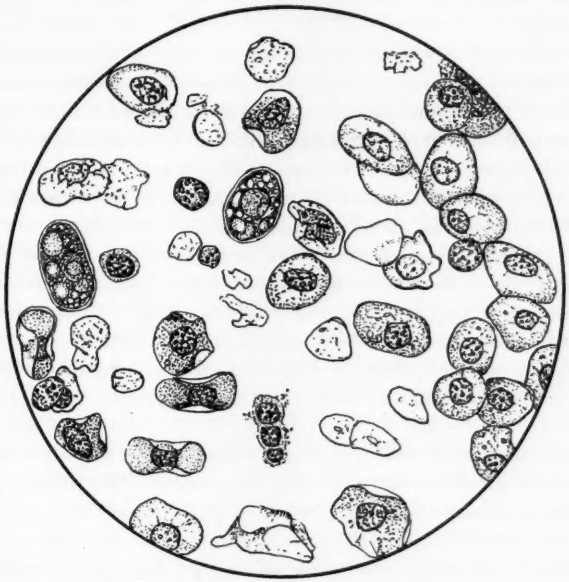

Fig. 3. Typical cells from the blood of a 9½-day chick embryo, exposed to 4 R.D. unfiltered X-rays, and allowed to survive 6 hours after the exposure. Some large oval cells containing refractile granules of varying size are shown. These are seen in the control as well as in the irradiated specimens and are probably detached entodermal cells from the yolk sac, laden with yolk granules undergoing absorption. Many of the erythrocytes are distorted and fragmented.

the blood stream into the general circulation, where under normal conditions they will break down still further and become absorbed.

Genital glands. Although differentiation of the gonads has commenced, it is not far advanced at this stage and changes produced by the action of X-rays are not so pronounced as in the adult ovary or testis. In the ovaries of the irradiated specimens the genital cells were in some cases not quite so clearly defined as in the controls, and the oöplasm was more granular. In some the capillary vessels were dilated both in the cortical and medullary zones. There were no obvious changes in either the genital or genitaloid cells of the testes of the irradiated specimens.

This lack of obvious changes in the genital cells of the experimental series is in marked contrast to the results obtained by Dantschakoff and Lacassagne (13). These authors describe complete destruction of the genital cells in both testis and ovary. The difference however may readily be explained when it is realised that these results were obtained by experiments carried out on chick embryos, (1) at much later stages of development, (2) that three separate doses were administered at intervals of 3 days, and (3) that the chicks were allowed to survive after the exposures up to periods of 17–21 days' total incubation.

DISCUSSION

Some of the most important work in this country of the effects of X-rays on mitosis was that of Strangeways (22) who exposed tissue-cultures obtained from the choroid of chick embryos of 6–7 days' incubation. Soft rays filtered through 2 mm. of cardboard were employed. He found in cultures fixed immediately after varying periods of exposure: (1) after 20 minutes fewer cells in prophase were present; (2) after 30 minutes cells in prophase were scarce; (3) cells in the later phases of mitosis begin to diminish in number after 25 minutes; (4) after 35 minutes only one or two are found; (5) if not exposed to X-rays longer than 30 minutes the cells already in prophase pass through the various stages of mitosis and the cells divide normally; (6) after longer exposures some of the chromosomes show granular changes and after an exposure of 50 minutes or longer some show lag in division both during metaphase and the passage of some of the chromosomes or their fragments to the poles of the spindle.

A second series consisted of cultures which were fixed after 80 minutes' incubation subsequent to varying periods of exposure. This period was selected by Strangeways because he found it allowed time for cells to pass through the phases of mitosis and complete their division: (1) after exposures of 20 minutes the appearance of dividing cells practically ceases; but (2) if cultures in which mitosis has ceased are returned to the incubator for some hours, cells in mitosis are again found, and unless too heavy a dose of X-rays has been given they become plentiful.

A synopsis of more recent work at the Strangeways Laboratory upon the action of radiations on tissue cultures has been given by Cox and Spear (12). Experiments by Strangeways and Fell (23), upon somewhat similar lines to our present work, show the disappearance of mitotic figures after 80 minutes' (post-radiation) incubation, and their re-appearance after 24 hours. In our experiments complete disappearance of mitoses was noted 2 hours after a single exposure, and re-appearance in specimens fixed after 4, 6 and 24 hours' (post-radiation) incubation.

Our observations thus completely agree with the results previously obtained by Canti and Donaldson (2), who, working with radium on tissue cultures from chick embryos, found mitoses present after 1 hour's exposure,

but absent after 2 hours and longer periods. If however the radium was removed after an exposure of 2–3 hours, mitoses gradually returned in the course of a few hours.

In none of their experiments was there any evidence of the radium producing an increase in the number of mitoses.

Spear (18, 19, 20, 21) concludes from his own experiments that the pre-mitotic stage is the most vulnerable phase of the nuclear cycle, so far as radiations are concerned.

It will be necessary here to refer to the use of the term "embryonic tissue" with regard to its bearing on the physiological factors concerned in tissue radiation. Bergonié and Tribondeau[1] showed in 1906 that X-rays act with greater intensity on cells which are actively reproducing themselves than those which are dividing less rapidly and also that their action is greater on cells which are preparing for their functional activity than those which are quiescent. In applying this general law to the conditions met with in experimental work on the later stages of growing embryos one must not infer that a developing organ, such as the thymus or testis is more sensitive to the action of X-rays in all stages of its development than it is in the adult. It is a well-known fact that the thymus and the testis of the adult are extremely sensitive to X-rays. The sensitivity of the fully developed thymus, however, is due to the presence of a large number of lymphocytes, these being the specially sensitive elements in its constitution. In the early stages of development they are not present, consequently there is no *special* sensitivity of the organ at this stage. Moreover in the testes where spermatogenesis continues throughout adult life both factors enunciated in the law are present and the adult organ is accordingly particularly sensitive to radiations, whereas during that period of its development which follows the initial stage of proliferation in which the cells are in an undifferentiated, quiescent condition pending the active growth and differentiation which will take place later at the attainment of sexual maturity very little change is produced by exposure to X-rays. A more highly differentiated and functional adult organ may thus be actually more susceptible to X-rays than the less differentiated developing organ, and the small amount of change which is produced by the radiations on the embryonic gland confirms the validity of the law rather than refutes it. The term "embryonic tissue" as employed in the description of certain tumours is usually applied to a tissue composed of rapidly proliferating cells, of large size and rounded form, such as are seen in a morula, and it is this type of tissue which is referred to as "embryonic" in the first condition which is associated with special sensitivity to X-rays. The important second condition, namely the modification which the cells undergo, "dans la préparation des transformations fonctionelles," appears to be less generally known and apt to be forgotten in comparing the sensitivity of adult with embryonic organs. Thus the susceptibility of a tissue often appears to depend as much upon the number of cells in it which are dividing at any given time as

[1] *Vide*, Regaud et Lacassagne (17).

upon any special sensitivity of the tissue or organ itself. The tissues of an embryo at any particular phase of its development vary greatly in the rapidity of their growth in different parts of the embryo. It may be inferred therefore that all embryonic tissue is not equally sensitive. Further, because a tissue is embryonic it is not necessarily more sensitive than the same tissue in the adult.

Although the central nervous system of the adult is generally regarded as particularly insensitive to γ- and X-rays, this must not be accepted without reservation. Indeed, although Morowoka and Mott in epitomising their work on the action of γ-rays on the central nervous system, state that "no gross nervous *symptoms*[1] were reported" in the experimental animals, they nevertheless describe and figure very definite *structural* changes as the result of exposure.

That the young and developing central nervous system with its abundant mitoses should be much more sensitive than that of the adult is only what would be expected.

Although research by the methods of tissue culture occupies a deservedly prominent place at the present time, yet we think that experiments of the type we have described have considerable value. The tissues are irradiated as parts of a living organism existing under natural conditions, with an established circulatory system, and growing in interdependence with each other. The two methods are complementary the one to the other, and either method may afford confirmatory evidence of results obtained by the other.

SUMMARY

The action of X-rays on the living tissues of chick embryos, under the conditions of radiation employed in this series, appears to be purely destructive.

The full effect of the rays is not manifested immediately.

The effects of the rays were more pronounced in the specimens exposed to unfiltered rays than in the screened series.

The structures chiefly affected are:

(1) The cutaneous ectoderm and the vessels of the subepidermal tissue.

(2) The central nervous system and the epithelium of the sense organs.

(3) The genito-urinary system.

(4) The vascular system; this shows dilatation of capillary vessels, and a damaged condition of the endothelium and red blood corpuscles.

Embryonic tissues and organs in which differentiation is more advanced appear to be more susceptible to the action of X-rays than those which are less highly differentiated.

The cellular changes consisted chiefly of a thickening of the nuclear membrane, which was sometimes accompanied by pycnosis. A ground-glass appearance and vacuolation of the cytoplasm, with diminished capacity for staining with eosin. Irregularity and blurring of cell outlines, with a tendency towards fusion of cells.

[1] The italics are ours.

We were unable to detect any difference in the number of mitotic figures in the nuclei of the control specimens and that in specimens killed immediately after exposure to X-rays 4 P.D.

Of those allowed to survive for a period after exposure, *no mitotic figures were present in specimens incubated for 2 hours subsequent to the exposure.*

In specimens allowed to survive 4 hours, mitotic figures were abundant, and in those which were allowed to survive 6 or 24 hours the number present was approximately equal to that in the controls, but there was irregularity in the disposition and form of the chromosomes.

No appreciable difference in the number of mitotic figures was apparent between the specimens exposed to filtered and unfiltered rays.

It appears that a single exposure to X-rays 4 P.D. produces a temporary inhibition of mitosis, but after 2 hours' incubation subsequent to the exposure, a recovery of the power of the cells to divide takes place, similar to that which has been previously demonstrated by Strangeways, Canti and Spear in both chick embryos and tissue-cultures.

Attention was drawn to the danger of mistaking normal processes of proliferation of cells and degeneration of tissue elements which occur in the ovular membranes, gonads and mesonephros of chick embryos about the 9th day of incubation for the effects of X-rays or radium, and the liability to error which exists in observations made upon the chorio-allantoic membrane.

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THE NON-METRICAL MORPHOLOGICAL CHARACTERS OF THE SKULL AS CRITERIA FOR RACIAL DIAGNOSIS

PART IV. THE NON-METRICAL MORPHOLOGICAL CHARACTERS OF THE NORTHERN CHINESE SKULL

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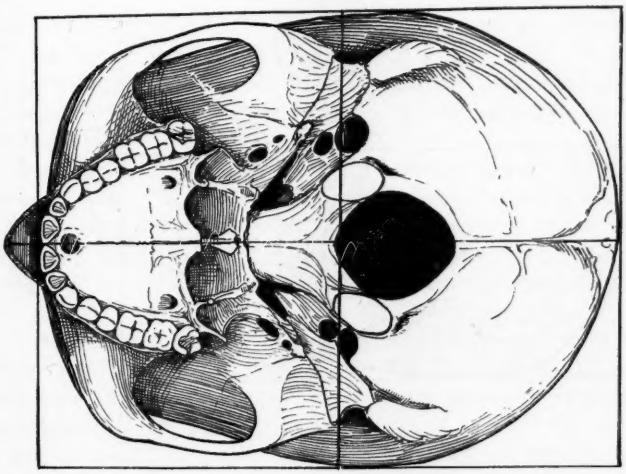
THE series of crania examined is that preserved in the Department of Anatomy of the Peiping Union Medical College. The skulls are those of the cadavera received in the dissecting room, and all details concerning sex, age and place of origin are accurately recorded. For permission to examine this series during my tenure of a visiting professorship at the Medical College, I am indebted to the authorities of the College and to Profs. Davidson Black and Droogleever Fortuyn, respectively Head and Acting Head of the Department of Anatomy. My observations on the crania are recorded without regard to the metrical examination, which is conducted as a routine by the staff of the department, and which will doubtless reveal many interesting features not embraced in the present survey.

The skulls were taken in their numerical order in the series: all crania that were not completely adult and all those that showed any pathological condition or were imperfect in some detail were eliminated. In this way a series of 100 perfect specimens was examined. Unfortunately the collection is deficient in the skulls of adult women and only seven are included in this series. Since numerically the female skulls are so insignificant, no attempt has been made to estimate the sexual distribution of the various morphological characters.

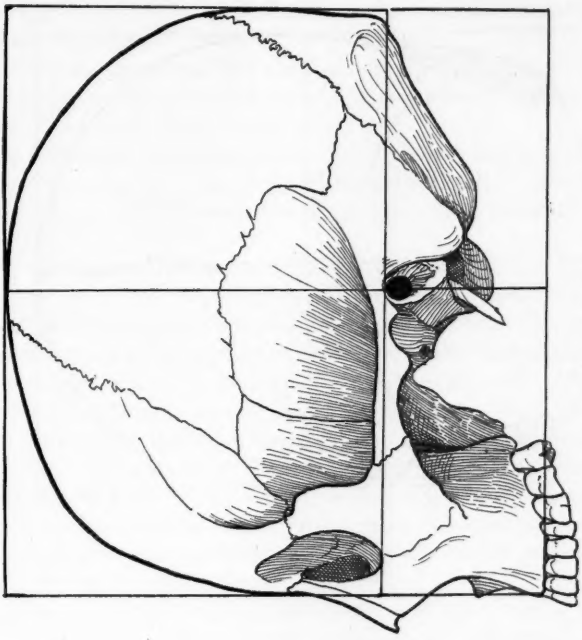
The sexual characters of these skulls are extremely ill differentiated and, judged by the standards applicable to European crania, a very large number of the males would be classed as female. In many cases this extreme femininity of the male skull is surprising. That shown in fig. 8 would probably be diagnosed by most physical anthropologists as female, yet it is that of a Chinese soldier 29 years of age, and is representative of a very large proportion of the smaller male skulls. The morphological characters of the skull would seem to be merely symptomatic of the general poor development of secondary sexual characters in the Chinese male.

(1) *Cranial form.* Of the whole series, 61 per cent. were obviously of an ovoid outline viewed in norma verticalis, while 39 per cent. approximated more nearly to a true oval. Of the sixty-one ovoid skulls, forty-nine were classed as



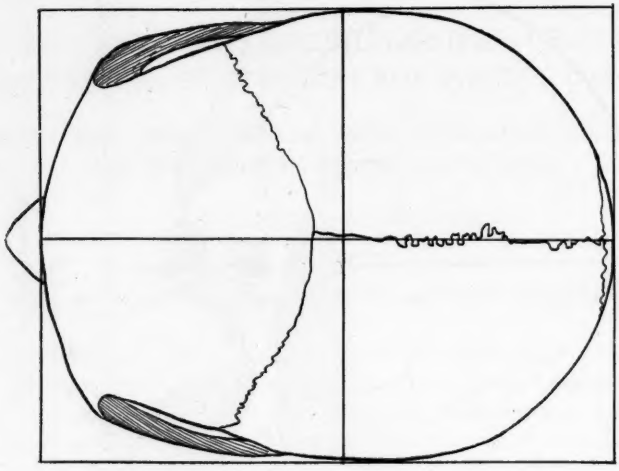
Chinese skull ♂

Fig. 1. Norma basalis. Typical Northern Chinese male.



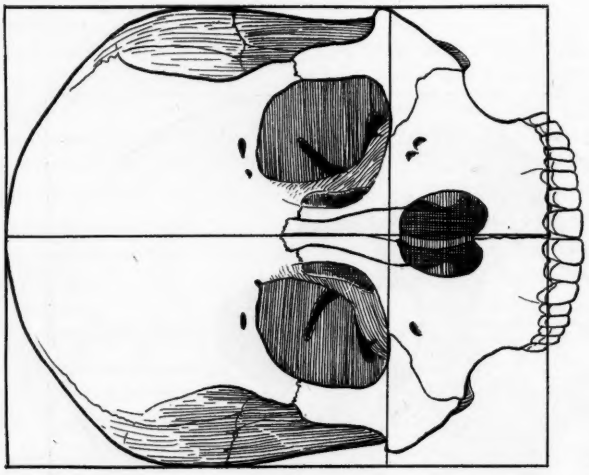
Chinese skull ♂

Fig. 2. Norma lateralis.



Chinese skull ♂

Fig. 4. Norma verticalis.



Chinese skull ♂

Fig. 3. Norma facialis.

broad ovoids and twelve as somewhat narrow ovoids. Of the thirty-nine oval skulls, twenty-eight were broad, approaching a rounded contour, and eleven were somewhat narrow.

(2) *Cranial asymmetry.* It is a rather noteworthy feature of this series that when asymmetry occurs it is usually of very considerable degree, the distortion of many of the skulls being remarkable.

Of the whole series, 33 per cent. showed no very striking degree of asymmetry as estimated by inspection of the contour of the vertex: 46 per cent. showed obvious normal asymmetry and 21 per cent. were of the reversed type of asymmetry.

(3) *The sutures* of the vault of the skull are distinguished by the fact that, though the excursions made by the dentations are usually of very limited extent, the dentations themselves are extremely fine. The general sutural pattern of the skull may be said to be simple, in that the course of the suture lines undergoes but little deviation: but combined with this simplicity of course is a considerable degree of very fine serration. In 34 per cent. an extremely simple sutural pattern was combined with less than usual serration of the sutures of the vault. In 63 per cent. a simple sutural pattern was combined with the typically fine serrations and in only 3 per cent. did complication of pattern and complexity of fine serrations exist. The metopic suture persisted in 5 per cent.: the ages of the individuals in whom this persistence occurred being 47, 77, 20, 50 and 25 years respectively.

(4) *Ossa suturarum* were present in 38 per cent. of the whole series. For the most part they were small sutural inclusions, the largest recorded being a median lambdoid inclusion measuring 40 × 35 mm.

Lambdoid ossicles occurred in thirty-three skulls. In six cases the inclusion was median, in fifteen the ossicles occurred bilaterally, in seven on the left and in five on the right side only. No true interparietal was present in any skull and most of the inclusions were small.

Ossicles in the *occipito-mastoid* suture occurred in nine instances. In five cases they were bilateral and approximately symmetrical and in four cases they were present on the right side only.

Coronary ossicles were present in three skulls; all were small and single and were confined to the pars complicata of the right coronary suture.

No ossicles of any kind were present in 62 per cent. of the whole series.

(5) *The pterion* was of the normal type in 95 per cent. The contact of the alisphenoid with the parietal was usually over a wide area: in ten skulls it was over 15 mm. and in one it extended for 27 mm. In only one case of normal contact could the area be described as unusually narrow. In one instance a true stellate junction occurred, in one there was temporo-frontal contact over a small area on the left side and in three the abnormal contact was present bilaterally.

(6) *Epipteric bones*, either unilateral or bilateral, were present in 28 per cent. of the whole series of skulls. They were situated bilaterally in 5 per

cent., on the right side only in 7 per cent. and on the left side only in 16 per cent.

(7) *Supra-orbital foramina, notches and grooves.* The most common condition was the existence of a well marked notch upon both sides. This was present in 61 per cent. and in seventeen of these cases the typical condition was complicated by the presence of additional small notches or foramina.

Bilateral foramina were present in 15 per cent. and in four of these cases small additional notches or foramina were present. The condition differed upon the two sides in 24 per cent., of which in ten cases the foramen was on the right and the notch on the left and in fourteen the condition was reversed. Of these asymmetrical cases seven were complicated by the additional presence of small accessory notches or foramina. In only one case were well-developed frontal grooves present and in this instance they extended as far back as the coronary suture.

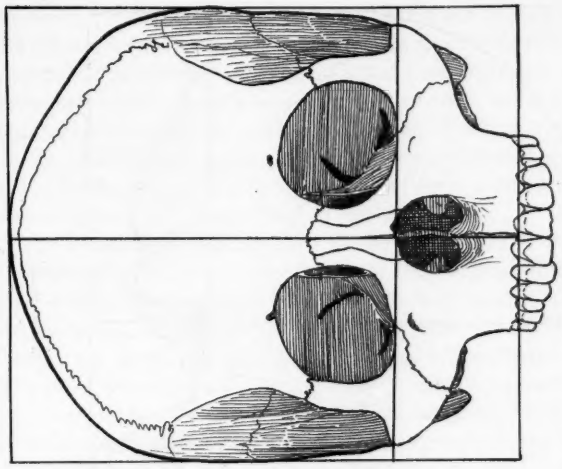
(8) *Foramen ethmoidale anterius.* In the whole series of 100 skulls the inner wall of the orbit was perfect and an unusual degree of assurance is therefore given to the observations upon its condition. The foramen was situated in the suture line between the frontal and ethmoid in 87 per cent. In 10 per cent. it penetrated the frontal, well above the suture, on both sides. In 3 per cent. the frontal site was unilateral, twice on the left side and once on the right. In no case did the canal penetrate the lamina perpendicularis of the ethmoid.

(9) *The sutures on the inner wall of the orbit.* These could be followed in every case and no anomaly was met with. The contact between ethmoid and lachrymal is very extensive, and in no instance was there any tendency to develop a fronto-maxillary articulation. The inflation of the ethmoid is carried to a very high degree in these skulls.

(10) *The spheno-maxillary fissure.* In general the fissure is narrower than that described and depicted in text books dealing with the European skull. In 72 per cent. the fissure was of the narrow type and in nineteen of these cases the narrowing was extreme. In 26 per cent. the narrow fissure was widened in its lower and outer portion and in 2 per cent. it was wide in the whole of its extent.

(11) *The form of the orbit.* Well marked obliquity of the orbit characterised 99 per cent. of the skulls. In seventeen cases the obliquity was extreme: in twenty-one the right orbit appeared on inspection to be more oblique than the left; in nine the obliquity appeared to be greater on the left, and in the remainder the slope of the two orbits appeared to be equal. In only one case did the orbits approach to a condition that could be described as approximately level.

There are certain additional features of the orbital region that are very characteristic of this series of skulls (see fig. 9). (1) The region of the glabella is typically flat or evenly curved in a lateral direction. (2) Below this, the nasal portion of the frontal is prolonged, flattened and with its lateral margins nearly parallel. (3) Inflation of the ethmoid and lachrymal regions is highly



Chinese skull ♀

Fig. 6. Norma facialis.

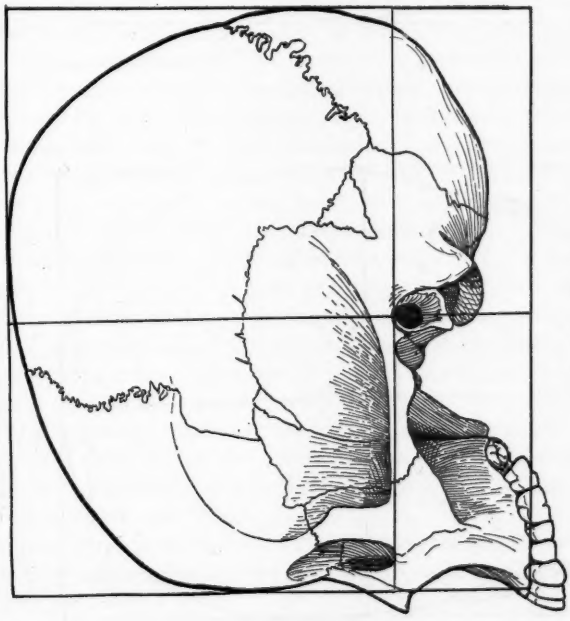


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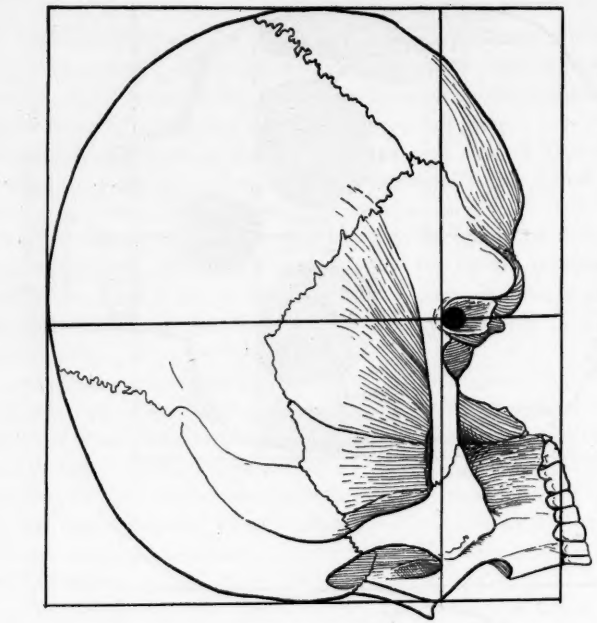
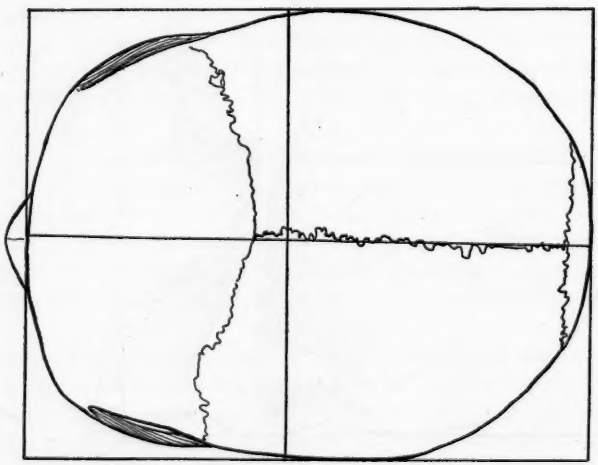
Fig. 5. Norma lateralis. Typical Northern Chinese female.



Chinese skull ♂

Fig. 8. Male skull with very indeterminate masculine characters, such as are frequent in the series.



Chinese skull ♀

Fig. 7. Norma verticalis.

developed and this condition is associated with (4) protrusion of the mesial wall of the orbit, (5) shallowness of the inner and lower portion of the orbital cavity and (6) the forward direction of the fossa sacci lachrymalis. The fossa sacci lachrymalis and canalis lachrymalis are of very large size and the fossa, viewed in norma facialis, is unduly conspicuous. The crista lachrymalis posterior is commonly extremely prominent and lies lateral, as well as posterior, to the crista anterior. An uncinate process is occasionally developed upon the lateral margin of the crista posterior (see fig. 10). The crista anterior is usually extremely thin and may even be perforated (see fig. 11).

These very remarkable conditions of the lachrymal sac in the Chinese are sufficiently distinctive to be of importance in the surgery of the orbit. My colleague Dr Arnold Pillat, Professor of Opthalmology in this Medical School, has for long embodied them in his course of instruction and I find them equally well marked in the skulls from certain archaic burials in North China.

(12) *The infra-orbital canal.* A single discrete canal was present upon both sides in 84 per cent. In 14 per cent. an additional small foramen was present: in nine of these cases the small accessory foramen was present bilaterally, in three it occurred only on the left and in two on the right side. The foramen was doubled only in two instances in the series.

(13) *The form of the jugal.* In only one case was the malar subdivided. The separated hypomalar portion was not symmetrical upon the two sides and the anomaly hardly fulfils the conditions of a bilateral zygomaticum bipartum. The form of the jugal is very characteristic. It is typically large, prominent, and everted at its lower margins. The prominence below and behind the fronto-malar suture (best known as the processus temporalis) is unusually well developed, the thickness of the post-orbital bar being far greater than is usual in European skulls of comparable build. In the whole series 91 per cent. possess the typical racial form of jugal that may be described as widened laterally, deep from above downwards and everted at the lower margin. In 9 per cent., though the eversion is well marked, the depth of the bone is not striking.

(14) *Nasal bones.* Although considerable variety exists in the form of the nasal bones, there is a very definite type that characterises the series as a whole. The individual nasal bone is elongated (over 25 mm.), expanded at the naso-frontal suture (which is situated some distance above the fronto-maxillary suture), contracted at about the upper third of its length and expanded again at its lower free margin. The upper extremities are usually equal in breadth and typically the two bones meet each other at a very slight angle (not peaked). Commonly they continue the axis of the nasal process of the frontal with but little angle at the nasion, and as a rule they are somewhat flat in the whole extent of their length (not tilted).

The typical form of the individual bones was present in 86 per cent. In 9 per cent. they were abnormally short and in 5 per cent. abnormally narrow for the series.

In 49 per cent. they were typical in both form and orientation. In 22 per

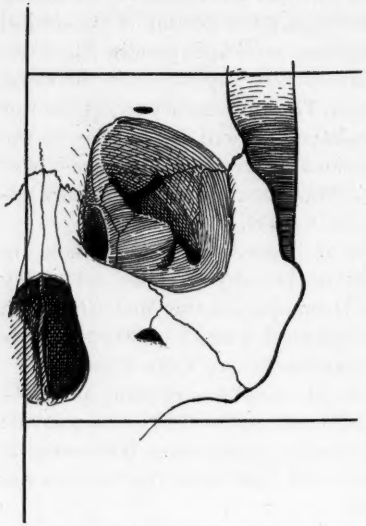


Fig. 9. The characteristic features of the orbital region.

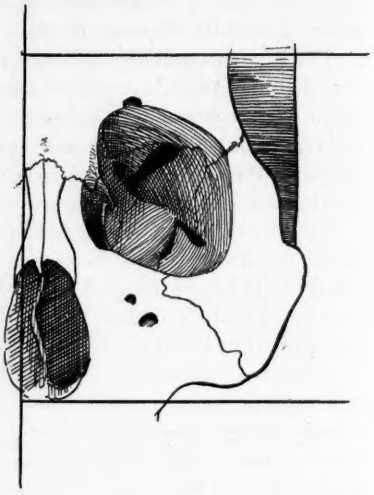


Fig. 10. Development of processus uncinatus on the crista lachrymalis posterior. (No. 71.101 bilateral.)

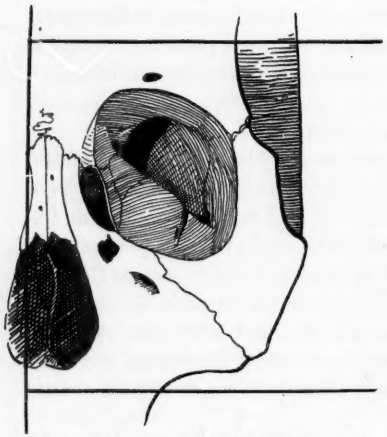


Fig. 11. Perforation of the crista lachrymalis anterior. (No. 64.91 bilateral.)

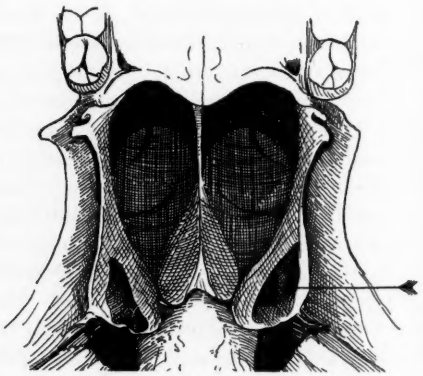


Fig. 12. Fossa in the base of the lamina pterygoidea media.

cent. they were unusually peaked, in 18 per cent. they were unusually tilted and in 7 per cent. both the peaking and the tilting were exaggerated.

(15) *The nasal aperture* varied so much in form that no particular type can be described as normal for the series. The actual aperture may be high or low, broad or narrow and its margins vary from perfect sharpness to almost complete guttering. In 25 per cent. the margins are single and sharp, culminating in a more or less developed spina nasalis. In 18 per cent. the margins though single are rounded and the spina nasalis is not represented by a prominent median spine. In 13 per cent. the margins show that degree of doubling that is best termed infantile. In 24 per cent. the doubling of the margins is well marked. In 18 per cent. the doubling approaches a definite guttering and in 2 per cent. the guttering is fully developed. The formation of the nasal margins showed no correlation with the form of the nasal bones, nor even with that of the nasal aperture.

(16) *The nasal septum.* This series of skulls is probably unique in the fact that in every example the bony septum is sufficiently complete for a diagnosis to be made as to the direction and degree of deflection. In only 14 per cent. was the septum truly median in the whole of its extent. It deviated to the left side in 44 and to the right in 42 per cent.

(17) *The foramen ovale.* The foramen is typically situated some distance from the posterior margin of the sphenoid. Upon both sides it was normal in shape, size and position in 61 per cent. It was recorded as being abnormally large (even up to 11 × 6 mm.) in 26 per cent. and abnormally small in 5 per cent. In every case in which the foramen was unusually small a foramen of Vesalius was present. The foramen was normal in shape and size, but directed laterally by the partial or complete formation of a pterygo-spinous bar, in 4 per cent. In 3 per cent. it was confluent with the foramen lacerum medium (two bilateral and one on the right side only): and in 3 per cent. it was confluent with the foramen spinosum (two on the left side and one on the right).

(18) *The foramen of Vesalius.* This was present on both sides in 14 per cent.; on the right side only in 11 per cent. and on the left side only in 8 per cent. It was absent upon both sides in 67 per cent.

(19) *The foramen spinosum* is typically situated some distance medial to the spina angularis. It occurred as a completed bony canal, normal in size and situation, in 43 per cent. It was deficient below on both sides in thirty-three, on the right side only in six and on the left side only in six.

It was confluent with the foramen lacerum medium in 8 per cent. (two bilaterally, three on the right and three on the left). It was confluent with the foramen ovale in 3 per cent.

In four cases the lower opening of the foramen was displaced by the partial or complete formation of a pterygo-spinous bar. In one case it was entirely absent upon both sides and in this instance the grooving inside the skull showed that the arteria meningea media had entered through the apex of the sphenoidal fissure.

(20) *The spina angularis sphenoidei.* The spina angularis, as a dependent prominence of the processus angularis, is absent in 3 per cent. In 10 per cent. it is only slightly developed and in 87 per cent. it is large and prominent.

In those cases in which it is well developed it is present as a sharp spine in thirty-two, as a smooth, nipple-shaped process in twenty-three, as a linear elevation in nineteen and as a rough irregular prominence in thirteen. In one of those cases in which it was developed as a smooth process it was distinctly bifid upon both sides. When it exists as a prominent linear process it is usually associated with a partial pterygo-spinous bar.

(21) *The laminae pterygoidei* have a very distinct racial form in that they are extremely upright (when viewed from the base); that the medial lamina is but little developed and that the lateral lamina is elongated (20 mm. or more) only at its lower margin. In the whole series 63 per cent. conform to this type. In 37 per cent. the lateral lamina shares with the medial lamina the condition of under development as judged by the standards of the European skull. In 9 per cent. of the whole series there is a definite tendency to the formation of a more or less complete pterygo-spinous bar medial to the foramen ovale. In 7 per cent. the condition is bilateral and in 2 per cent. confined to the left side.

A very constant feature of the medial lamina is the deep pit which indents its expanded base. This is perhaps a modification of the *fossa scaphoidea* BNA, but it differs fundamentally from the classical form in that the fossa is not a part of the *fossa pterygoidea* BNA, but is definitely medial to the lamina pterygoidea media: indeed, in several examples, this deep pit would seem to co-exist with the true fossa scaphoidea of classical type. In this form it is highly characteristic of this series of Chinese skulls and a typical example is illustrated in fig. 12.

(22) *The jugular foramen.* In 10 per cent. of the whole series the jugular fossae could be said to be approximately equal upon the two sides. In 76 per cent. that of the right side was distinctly larger than that on the left and in 14 per cent. the left was the larger of the two.

(23) *The tympanic* typically develops a well marked vaginal process. The bony external auditory meatus is short and in its typical condition is thin in its medial portion and somewhat thickened at the meatal margin.

In three instances the external meatal notch was evident (in two bilaterally and in one on the right side only). In one case the external auditory meatus was abnormally narrow, but in no case did the development of exostoses produce any constriction of the canal.

(24) *The foramen of Huschke* was present in 12 per cent. In all cases the foramen was very small, the largest recorded being 3 mm. in diameter and in most cases it exists as a minute foramen only admitting a pin point.

Of the twelve cases in which it occurred, eight were bilateral and four were on the right side only.

One peculiar feature of this region of the skull is the characteristic inflation of the apex of the petrous which is present almost without exception in this

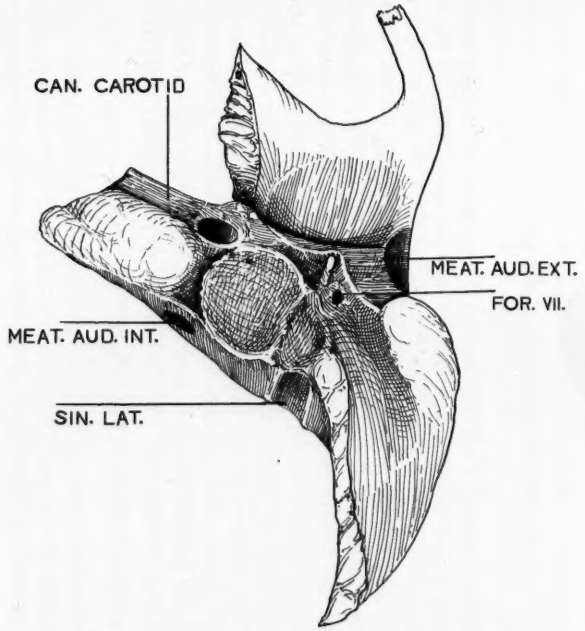


Fig. 13. Left temporal bone to show the inflation of the petrous apex.

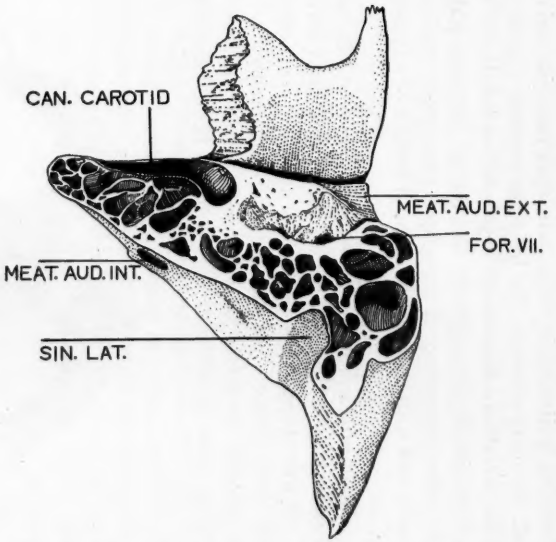


Fig. 14. Section of left temporal bone to show the distribution of air cells.

series. The inflation is situated in the petrous apex posterior and medial to the carotid canal. In many examples the inflation amounts almost to a minimal degree of bulla formation. A moderate degree of this inflation is illustrated in fig. 13. The condition is a remarkable one, for the air cells, which cause the rounded and swollen appearance of the petrous apex, are in continuity with the tympanic cavity and with the mastoid cells. A section of a typical example is shown in fig. 14.

(25) *The styloid processes* were present in 82 per cent. In those cases in which it was present it was large in thirty-three, small in thirty and rudimentary in nineteen. It was absent upon both sides in 18 per cent. and four (out of seven) females were among those showing complete absence.

(26) *The posterior condyloid foramina* were present bilaterally in 63 per cent. and among these twenty-four were noted as being unusually large. The

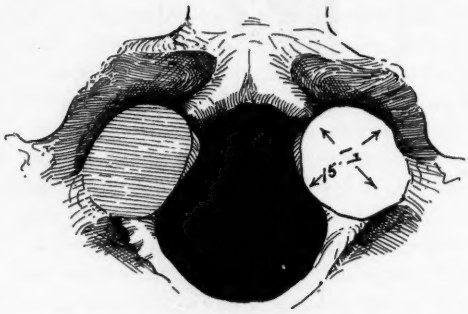


Fig. 15. The occipital condyles of skull No. 96.130.

foramen was present on the left side only in 16 per cent. (of which three were unusually large); and on the right side only in 8 per cent. (of which two were unusually large).

It was entirely lacking in 13 per cent. of the entire series.

Two other conditions of the occipital region are peculiarly characteristic of this series. The first is the frequency of a short, flat, and rounded form of occipital condyle, such as shown in fig. 15. The condyles at times appear almost in the form of those typical of the atlas, but even in the most marked cases there is no true assimilation of the atlas to the skull. The other noteworthy feature is the inflation and prominence of the lateral masses of the exoccipitals. The paroccipital process in these cases is not a roughened mass of bone, but a smooth inflated protuberance—the true *processus pneumaticus* of Hyrtl—and as such is almost invariably present in these skulls.

THE ARTICULATIONS OF THE CARPUS IN *CHIROMYS MADAGASCARENSIS* WITH REFERENCE TO CERTAIN OTHER LEMURS

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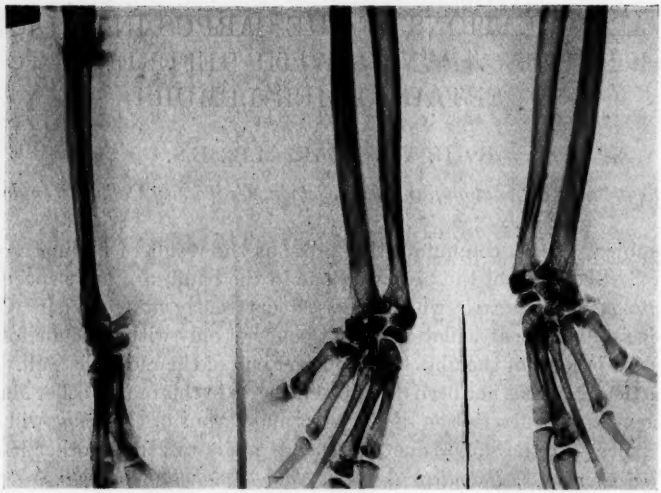
THE subject of this communication arose as the result of finding a curious mode of articulation of the pisiform bone in the hand of a male specimen of *Chiromys madagascarensis* which I dissected recently at University College. This consisted in the articulation of that bone not only with the cuneiform and the styloid process of the ulna but the lower end of the radius as well. As the latter articulation has not been described hitherto in this or any other Mammal, I consider a fuller description of the wrist and carpus of *Chiromys* will not be out of place. At the same time reference is made to certain other lemurs—*Loris lydekkerianus, Perodicticus potto, Galago maholi, Hemigalago demidoffi* and *Lemur*—for comparison. The account of *Lemur* is based on the works of Gregory (6) and Parsons (11), while that of the others is the result of my own observations.

In his classical monograph "On the Aye-aye," Owen (10) figures and describes the articulations of the wrist and carpus as follows: "The wrist bones are ten in number, including a supplemental sesamoid on the outer side of the scapho-trapezial joint. The scaphoid is the largest, presenting its convex articular surface to the outer two-thirds of the radial concavity, and articulating with the lunate which completes the wrist ball; at the distal surface it joins the intermedium, the trapezium and the trapezial sesamoid. The cuneiform offers a cup for the hemispheric end of the styloid process of the ulna and a flatter surface for the pisiform; this wrist bone is long and its articular surface is divided between the ulnar process and the cuneiform. The intermedium and cuneiform combine to form a cup for the ball common to the os magnum and the unciform and of which the latter bone constitutes the largest share. The intermedium articulates with the trapezoid. The distal series of carpals have the usual relations to the metacarpals." No reference is made in the description to the articulation of the pisiform with the radius. Mivart (9) and Flower (3) have made extensive studies of the skeleton of the Primates and other Mammals but make no reference to any such articulation of the pisiform.

THE CONSTRUCTION OF THE WRIST-JOINT IN *CHIROMYS*

The wrist-joint in *Chiromys* is formed above by the lower ends of the radius and the ulna and below by the scaphoid, semilunar, cuneiform and pisiform. It is separated from the distal radio-ulnar articulation by a strong interosseous



I. Lateral view. II. Antero-posterior view. III. Postero-anterior view.

Fig. 1. X-ray photograph of the wrist and carpus of *Chiromys*.

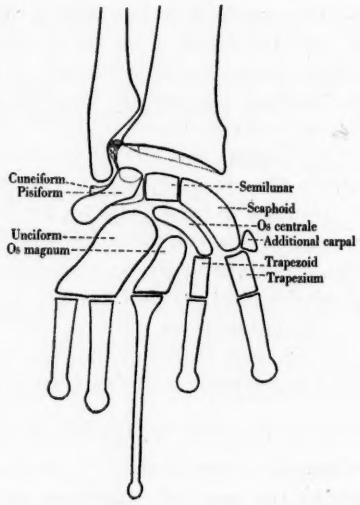


Fig. 2. A diagram to show the carpal elements of *Chiromys*.

ligament stretching from the medial margin of the lower end of the radius to the ulna. The anterior and posterior margins of this ligament are fibro-cartilaginous, while the intermediate greater part is fibrous. The posterior part passes from the radius to the interosseous ligament between the semilunar and cuneiform. A completely fibro-cartilaginous triangular disc, as it occurs in Man, is wanting in *Chiromys*. The cavity of the joint is divided into two compartments, freely communicating in front, by a septum which stretches from the interosseous ligament mentioned above to that between the semilunar and cuneiform bones. In the radial compartment the radius articulates with the scaphoid, semilunar and pisiform bones, these three together forming a convex condylar articular surface. The last-mentioned bone has the facet for the radius on the superior aspect of its outer end. In the ordinary position of the wrist-joint the radius is in contact only with the scaphoid and the semilunar, but when the joint is flexed it comes into articular relation with the pisiform. The ulnar compartment of the joint is formed by the globular lower end of the thick styloid process of the ulna, articulating in a hemispherical socket looking backwards and formed by the cuneiform and the pisiform, the former bone taking the greater share. The cavity of the piso-cuneiform articulation is in communication with this compartment.

THE ARTICULATIONS OF THE CARPUS IN *CHIROMYS*

To the description of the carpal elements as given by Owen, the following few observations may be added. The cuneiform is almost entirely covered on its volar aspect by the pisiform, so that it is clearly visible only from the dorsal aspect of the carpus. The latter bone is large and has three articular facets, viz. for the cuneiform, the ulna and the radius. The articulation of the bone with the radius appears to be unique. Even in the extinct Marsupial, *Diprotodon australis* mentioned by Gillies (5), where the pisiform is the largest member of the carpal series and takes a prominent part in the formation of the wrist-joint, it is not known to articulate with the radius. In *Chiromys* it presents a small, nearly circular convex facet on the superior aspect of its radial end, which comes into contact with the radius as well as the anterior part of its interosseous ligament when the wrist-joint is flexed. The inner end of the pisiform projects as a thick process which provides a strong attachment to the tendon of the flexor carpi ulnaris and the anterior annular ligament of the wrist. From the distal part of the root of this process the piso-hamate and piso-metacarpal ligaments extend to the unciform and the base of the 5th metacarpal respectively.

In the intermediate row there are two carpal elements. Of these the larger one referred to by Owen as "intermedium" is situated between the scaphoid and semilunar above and the trapezoid, os magnum and unciform below. In shape it resembles a second semilunar. The smaller of the two is referred to by Owen as "a supplemental sesamoid on the outer side of the scapho-trapezial

joint." It is situated between the scaphoid and the trapezium, articulating with both but mainly with the former. It is doubtful if it can be regarded as a radial sesamoid, for it is not developed in the tendon of the flexor carpi radialis but is situated on its outer side, giving attachment to a slip of the tendon of the extensor ossis metacarpi pollicis. From its position between the scaphoid and the trapezium it would appear to be more probably a second member of the central series, displaced to the outer side of the carpus.

In the distal row the only noteworthy feature is the small size of the os magnum and the compensatory large size of the unciform. These two bones together form proximally a ball fitting into a socket, in the formation of which the intermedium, a small part of the semilunar (not mentioned by Owen) and cuneiform take part. The unciform forms the major part of this ball. According to Gregory (6) the increased size of the unciform is the result of two factors: (1) a wide divergence of the pollex giving rise to a crowding of the carpal elements on the ulnar side, (2) the elongation of the 4th and 5th digits which articulate with it distally. Its articulation with the os centrale is considered by Gregory as a specialisation of the Lemuroidea alone among the Primates. In this respect *Chiromys* shows one more evidence of its lemurine affinity not hitherto pointed out.

The trapezoid is small and articulates proximally with the os centrale only.

COMPARISON WITH OTHER LEMURS

From the description given by Gregory (6) and Parsons (11), the articulations of the wrist and carpus in Lemur are similar to those of *Chiromys*, except that the pisiform takes no part in the radio-carpal articulation. No mention is made of an additional carpal element of the central series on the radial margin of the carpus.

In the Galaginae—*Galago maholi* and *Hemigalago demidoffi*—the articulations are similar to those of Lemur. As in the latter the pisiform takes part in the ulno-carpal compartment of the wrist-joint. There is, however, an additional carpal element on the radial margin of the carpus as in *Chiromys*.

In the Lorisinae—*Loris lydekkerianus* and *Perodicticus potto*—the pisiform is smaller and the styloid process of the ulna relatively slender. The latter articulates only with the cuneiform. The articulation of the pisiform is restricted to the cuneiform only and the cavity of this joint is in communication with that of the ulno-carpal as in the other lemurs. Besides the intermedium and the additional carpal on the radial margin of the carpus, there is an os ventrale carpi which, however, is not a member of the carpal series but an ossification in the anterior annular ligament. This bone converts the carpal arch into a nearly complete bony tunnel, through which the flexor tendons pass into the palm of the hand.

An os centrale has been described in all Primates except gorilla, chimpanzee and Man. In Man, according to Broom (1) and Frazer (4), this bone can

be detected in the early embryo, and it occasionally occurs in the adult as an abnormality. The additional carpal element, described above, is present in all the lemurs examined by me. In all the forms it is situated on the radial margin of the carpus opposite the interval between the scaphoid and the trapezium, articulating with both, and has no connection to the tendon of the flexor carpi radialis. Wood Jones figures it in exactly a similar position in the carpus of *Tarsius* (13), but says that it does not articulate with any bone, being held in place by fibrous tissue. It is not situated in tendon but enveloped in the capsule of the carpal articulation. He further suggests that he can homologise this bone with only a second os centrale (13). According to Le Gros Clark it is also present in *Tupaia*. He considers it as probably a common feature in the carpus of arboreal Mammals and further suggests that it might be the homologue of the tibial sesamoid or "prehallux" such as that described by him in *Ptilocercus*. From the nature of its articulations and the absence of any connection with the tendon of the flexor carpi radialis I am inclined to agree with Wood Jones in considering it as a second os centrale displaced to the outer margin of the carpus. The presence of two carpal elements of the central series appears to be a general occurrence among the Lemuroidea. This statement, however, requires further confirmation from observations on other lemurs.

In the Lemuroidea the pisiform is of three different types: (1) in the Lorisinae it articulates with the cuneiform only as in Man. It differs from Man, however, in that this joint cavity is always in communication with the ulno-carpal articulation; (2) in the Galaginae, *Lemur* and *Chiromys* it articulates with the ulna as well, forming part of the ulno-carpal articulation; (3) in the last-mentioned animal it articulates with the radius also, forming part of the radio-carpal articulation.

In all the forms dissected by me the unciform exceeds the size of the os magnum and articulates above with the os centrale, semilunar and cuneiform bones. In *Tarsius* and the Anthropoidea the unciform becomes smaller and fails to reach the os centrale. Herein, the Lemuroidea—both Lemuriformes and Lorisiformes—show an evidence of a specialisation in virtue of which they have diverged from the main line of the Primate evolution.

As in *Chiromys*, in none of the above-mentioned forms can a triangular fibro-cartilaginous disc of the form occurring in Man be said to exist. Its beginnings are, however, to be seen in the fibro-cartilaginous nature of the anterior and posterior margins of the interosseous ligament connecting the lower end of the radius to the ulna. With the development of an increased power of supination and pronation as in Man this ligament becomes more perfected and entirely cartilaginous, so as to form a triangular articular disc.

THE ORIGIN OF THE OS PISIFORME

Gillies (5), in a paper published in this *Journal* in 1929, has discussed the three theories concerning the origin of the pisiform bone, viz. (1) the pisiform as a sesamoid, (2) the pisiform as a vestigial post-minimus, (3) the pisiform as a member of the central carpal series. Basing his reasons on comparative study of certain reptilian forms—*Broomia, Sphenodon* and *Lacerta*—he concludes that the pisiform is a member of the central carpal series displaced to the proximal row. The observations of Frazer (4) on the development of carpal elements also support this theory, for he says that "the pisiform is formed with the other carpal elements of which it would seem to be one, rather than a sesamoid formation." The articulations of the pisiform with the ulna as well as the radius in *Chiromys* might suggest a further confirmation of this view. The pisiform appears to be an intrinsic member of the carpal series and not a mere sesamoid. A true sesamoid bone such as the patella is developed in the substance of the tendon of a muscle and will form, at most, a single articulation which is fixed in its relation to one bone.

SUMMARY

1. The present paper is based upon an examination of the wrist and carpus of *Chiromys madagascarensis, Perodicticus potto, Loris lydekkerianus, Galago maholi* and *Hemigalago demidoffi.*

2. In all the forms, both radius and ulna take part in the formation of the wrist-joint. In the Lorisinae the scaphoid, semilunar and cuneiform bones form the distal articular surface; in the Galaginae, *Lemur* and *Chiromys* the pisiform as well. In the last-mentioned animal the pisiform articulates with both ulna and radius.

3. There are ten carpal elements in all. Besides the usual eight occurring in Man, there are two ossa centralia, one situated between the scaphoid and semilunar above and the trapezoid, os magnum and unciform below; the other between the scaphoid and the trapezium on the outer margin of the carpus.

4. The unciform is largely developed at the expense of the os magnum, and articulates not only with the cuneiform and the semilunar but with the intermedium as well. This is a specialisation in the Lemuroidea alone among Primates.

5. The pisiform is relatively large in *Chiromys.* It articulates with the cuneiform, ulna and radius. The presence of so many articulations might suggest an additional confirmation of the carpal theory of origin of this bone.

This work was carried out in the Department of Anatomy and Embryology, University College. I wish to express my gratitude to the several anatomists of this Institution for the facilities and suggestions given to me, particularly to

Prof. G. Elliot Smith, F.R.S., Prof. J. P. Hill, F.R.S., and Prof. H. A. Harris, D.Sc. I also wish to thank Mr Frederick Melville, of the X-ray Department of the Institution, for the X-ray photographs.

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ANATOMICAL NOTES

THE ORIGIN OF THE FIRST DORSAL INTEROSSEOUS MUSCLE OF THE FOOT

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In the standard text-books of anatomy the first dorsal interosseous muscle of the foot is described as arising by medial and lateral heads from the adjacent sides of the first and second metatarsal bones.

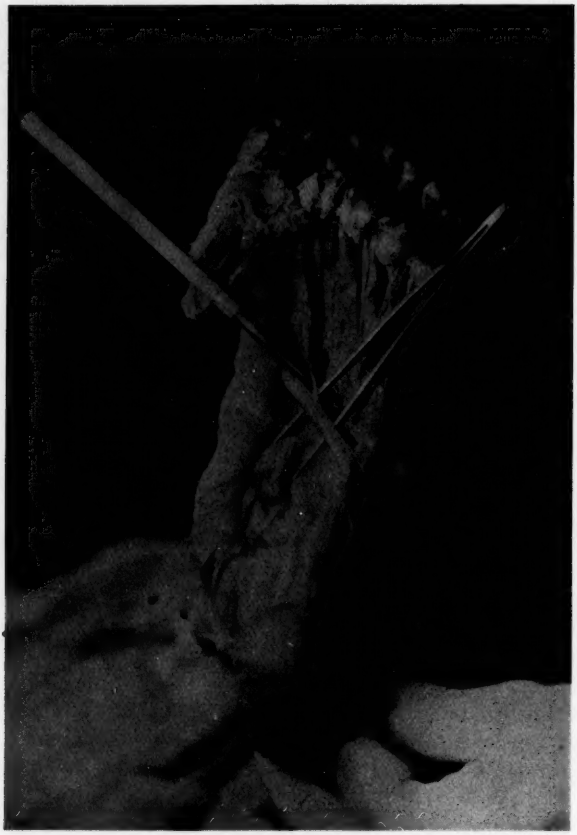

Fig. 1. Plantar view of the left foot to show the origin of the medial head of the first interosseous by means of a tendinous slip from the tendon of the peronaeus longus.

Toldt's *Atlas of Human Anatomy* (1) contains an illustration in which the medial head of the muscle appears as if it had a tendinous origin from the peronaeus longus tendon, but no attention is drawn to it.

Bryce (2) mentions that the first dorsal interosseous receives fibres of origin from the peronaeous longus tendon at its insertion. He does not make it quite clear which head receives these extra fibres.

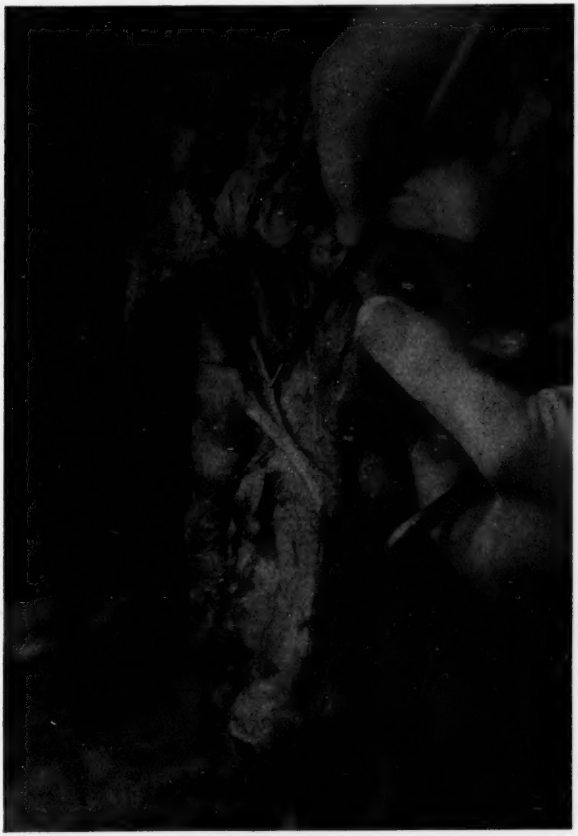

Fig. 2. Plantar view of the left foot to show the relations of the tendinous origin and the absence of true attachment to the first metatarsal bone.

In a series of 27 feet from 15 male subjects, the precise origin of the muscle has been examined. The origin of the lateral head was found to be as commonly described, but in 20 dissections out of 27 (or 11 subjects of the 15 dissected) the medial head was found to arise by means of a tendinous slip from the peronaeus longus tendon as it (the tendon) passed along the peronaeal sulcus on the plantar surface of the cuboid bone. In these dissections the attachment of the medial head to the first metatarsal bone was by means of loose connective tissue only. The seven

feet, where no tendinous origin was found, showed a direct muscular origin for the medial head from the proximal part of the medial side of the first metatarsal bone: in one subject the "tendinous" origin was found in the left and the "muscular" origin from the first metatarsal in the right foot. The thickness of the tendon of origin varied considerably. It was always enclosed in a mucous sheath continuous with that enclosing the peronaeus longus tendon and lay dorsi-lateral to the tendon of the peronaeus longus.

In the dissections made the relation of the first dorsal interosseous muscle to the remaining interosseous muscles of the foot was noted. One is struck with the obvious plantar position of the first dorsal in comparison to the dorsal position of the other three dorsal interossei. In short the first dorsal is in the same plane as the three plantar interossei. It is therefore suggested that the first dorsal be renamed the first plantar and the remaining interossei named in series with it.

Summary

1. The medial head of the first dorsal interosseous muscle of the foot takes origin, probably in a large percentage of cases, by means of a tendinous slip from the tendon of the peronaeus longus muscle.

2. It is suggested that the first dorsal interosseous muscle should be renamed the first plantar interosseous and the interossei regrouped into three dorsal and four plantar muscles.

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NOTE ON AN UNUSUAL TYPE OF CERVICAL RIB IN A LEMUR

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In the course of my dissections on *Perodicticus potto*, an African Lorisform lemur, I came across a pair of cervical ribs presenting some remarkable features which are worthy of record and fuller description. Reference to available literature showed no parallel case in any Primate or other Mammal. Most of the references to cervical ribs relate to Man, in whom they have been observed on numerous occasions in the adult and in various stages of development. Turner (4) refers to their occasional occurrence in the 7th cervical vertebra of the Cetacea, and in the 8th and 9th cervical vertebrae of *Bradypus tridactylus*. In all these cases, he says, the cervical ribs are not fully developed but remain in a rudimentary state. Mivart (3), in his paper on the axial skeleton of the Primates, gives no description of any cervical ribs.

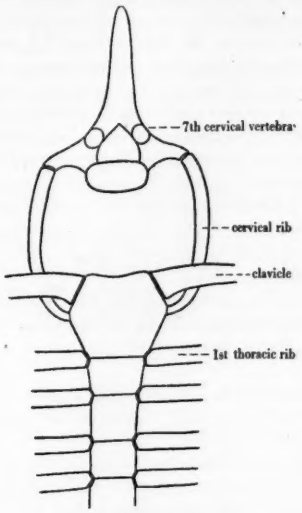

Fig. 1.

In *Perodicticus* there are normally fifteen ribs on either side, as shown in a skeleton in the Zoological Museum, University College, and as recorded by Flower (1). In the specimen described here there are seventeen ribs on either side, of which the first is a fully developed cervical rib in connection with the 7th cervical vertebra, and the last one is a lumbar rib articulating with the side of the body of the 1st lumbar vertebra. The cervical rib articulates posteriorly with the tip of the transverse process of the 7th cervical vertebra by means of a diarthrodial joint, but has no connection with the body (see fig. 1). In front it articulates with the side of the manubrium sterni through the medium of a costal cartilage. This articulation is immediately below that of the clavicle in the position of the normal 1st rib which is displaced to a lower level, namely to the junction of the manubrium and the gladiolus of the sternum. In

appearance it is more rounded and more slender than the 1st thoracic rib below it. The latter is broad and strong and resembles in every respect the normal 1st thoracic rib. The two cervical ribs are symmetrically developed and virtually take the place of the normal 1st thoracic ribs at the inlet of the thorax.

The various muscles that are normally attached to the 1st thoracic rib are transferred to this cervical rib. The subclavius muscle arises from it in front and part of the first digitation of the serratus anterior more laterally. The rectus abdominis and the two supracostal muscles are inserted into it just lateral to its cartilage, while part of the scalene muscle is inserted somewhat more laterally. This muscle in *Perodicticus* cannot be divided into scalenus anterior, medius and posterior, for the whole mass is situated behind the subclavian artery. It has two parts; a superficial passing to the 4th, 5th, 6th and 7th ribs deep to the serratus anterior and a deeper part inserted into the 1st rib (i.e. cervical in this case). The latter is pierced by the respiratory nerve of Bell. The brachial plexus is not prefixed but is formed in the normal way extending from the 5th cervical to the 1st thoracic nerve. There is no indication in the intrinsic musculature of the hand of any undue pressure on the lower segment of the brachial plexus. The subclavian vessels pass over the cervical rib in their course from the root of the neck to the axilla.

The transverse process of the normal 7th cervical vertebra in *Perodicticus* is usually imperforate as is generally the case in other lemurs. Consequently there is no anterior tubercle or costal element. In this respect the 7th cervical vertebra of this specimen is to be regarded as normal except for the cervical rib at the tip of its transverse process. In the upper six cervical vertebrae the transverse processes are perforated by the vertebral artery and end in well-marked anterior and posterior tubercles except in the first two or three vertebrae where the two tubercles are fused.

The sternum is long, narrow and flattened, and consists normally of nine segments of which the manubrium is the broadest. In this specimen there are ten segments, the additional segment being probably the one below the manubrium and derived from the presternum. At the junction of the 1st and 2nd sternebrae of the mesosternum the bone is bent almost to a right angle, and just opposite this there is a deep flexure of the thoracic spine, concave forwards.

There were no other developmental defects. The bladder was found to be strongly contracted and its walls fasciculated. This, on opening the viscus, was found to be due to the presence of a calculus, from which the animal must have suffered for some time.

The most interesting features in this cervical rib are:

(1) The manner in which it completely assumes the position normally occupied by the 1st thoracic rib at the thoracic inlet.

(2) Its articulation with the transverse process only of the 7th cervical vertebra.

(3) The position of its articulation with the manubrium, displacing the 1st thoracic rib to the junction of the manubrium and the first segment of the mesosternum.

Turner (5) states that the cervical ribs may arise in Man in two ways, viz.: (1) by separate ossification and excessive growth of the anterior transverse process of the 7th cervical vertebra; (2) by unusual development of the epiphyses at the tip of the transverse process, in which case the rib articulates only with the tip of the transverse process. In the former case the rib articulates both with the body and the transverse process. In *Perodicticus* the cervical rib has evidently developed according to the second mode of formation. According to Turner (5) the former type is homologous with the inferior roots of the transverse processes in Birds, and with the cervical ribs in crocodiles, while the latter type corresponds to the rudimentary ribs connected with the 8th and 9th cervical vertebrae of *Bradypus tridactylus*. Ribs articulating only with the tip of the transverse process are described by Flower (1) in the Cetacea—in the posterior thoracic region of the dolphin, *Globiocephalus melas*.

The mode of articulation of the cervical rib with the manubrium in the usual position of the 1st thoracic rib is unique. It appears that the presternum in this specimen of *Perodicticus* is really split into two segments, namely, the one referred to above as the manubrium and the other the first segment of the mesosternum. If that be so it is possible that the lower segment of the presternum has been absorbed into the mesosternum but reveals its true nature by the position of the articulation of the 1st thoracic rib. In the majority of the Mammalia the 1st rib is constant in its articulation with the manubrium. It is unusual for the 1st rib to articulate with the junction of the manubrium and the mesosternum. The opposite condition is described by Keith (2) in *Hylobates*, where the manubrium commonly absorbs the first segment of the mesosternum, so that the joint (sternal angle) is at the level of the articulation of the third pair of thoracic ribs. The junction of the manubrium and the gladiolus which is normally at the level of the second pair of ribs may thus shift its position one segment caudally as in *Hylobates* or one segment cranially as in this specimen of *Perodicticus*. The former condition is the more common of the two, for according to Keith it may also be seen in other anthropoid apes though less commonly than in *Hylobates*. The cranial shift of the sternal angle (junction of manubrium and gladiolus) is rare and is probably found only in the presence of a complete cervical rib as in this instance. These anatomical variations confirm the view that the presternum as it occurs normally contains elements corresponding to cervical ribs as Albrecht (quoted by Keith) suggested many years ago.

Lastly it may be pointed out in the words of Turner, that "the cervical rib is only an individual peculiarity and is not to be regarded as evidence of generic or specific difference."

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REVIEWS

Studies on the Physiology of the Eye. Still reactions, sleep, dreams, hibernation, repression, hypnosis, narcosis, coma, and allied conditions. By J. GRANDSON BYRNE. (London: H. K. Lewis and Co.) 1933. Pp. xii + 416, 47 figs. Price 40*s.* net. Bibliography and index.

In this book the author presents his very extensive experimental evidence, the work of other investigations, the arguments and biological considerations which have led him to formulate a conception of neural interaction arising out of general biological needs.

His experimental enquiries have been directed to the mechanisms which govern the widening and the narrowing of the pupil, the palpebral fissure, and the lens, as well as proptosis and retraction of the eye as a whole. These present a uniform pattern and follow a developmental sequence, being in the first instance chemical, then chemico-neural—the action being initiated in the appropriate centre, and finally of the reflex type in which the activity is aroused from the centres by afferent and efferent impulses. In this latest stage the centres affect each other in a reciprocal manner.

Further, the author concludes that the reflex narrowing of the above-mentioned structures together with retraction, the parasympathetic action, is activated by critical proprioceptive impulses from the striated muscles of the body which pass then to the cortex and subcortical centres and through these exert their influence on the parasympathetic apparatus.

The sympathetic activities—the widening of the above structures and the advancement of the eye—are driven by afferent impulses mainly of an affective character. In this way each group functions as a unit and co-ordination and co-operation are established by their interaction with each other. In addition these two aspects of ophthalmic activity are the offshoots of the mechanism of approach and avoidance respectively and thus the eye, the great distance receptor, is on the one hand related to the more primitive aspects of these biological reactions while on the other it ministers to these same reactions at the higher psychic level.

This brief summary of the author's conception does not do justice to the vast amount of detailed experimental work an account of which occupies the greater part of the book. This part is extensive, detailed and most impressive. Its proper appreciation demands careful reading of each chapter.

The Thyroid Gland. Its Chemistry and Physiology. By CHARLES ROBERT HARINGTON, M.A., PH.D., F.R.S., Professor of Pathological Chemistry in the University of London. (London: Oxford University Press.) 1933. Pp. xii + 222, 28 figs. Price 15*s.* net.

A monograph on the thyroid by the present author is approached with unusual eagerness because of the great success which attended his chemical investigations. It is clear from the modest statements in this book that Prof. Harington in determining the chemical structure of thyroxine and accomplishing its synthesis achieved not only a great chemical triumph but also presented to all investigators a criterion by which many theories and speculations concerning thyroid activity could be tested.

The first chapter concerns itself with historical views on the action of the thyroid and with the current notion that it regulates the metabolic rate of the body.

The second is concerned with the general chemistry of the gland and gives the evidence for the statement that the thyroid owes its peculiar activity to the presence

in thyreoglobulin of a specific iodine compound which is probably not derived, directly at least, from any of the known amino-acids.

The author then proceeds, from a consideration of cretinism, goitre, etc., to the generalisation that a sufficiency of iodine is essential to the maintenance of the normal structure and function of the gland. A full discussion of the technical procedures by which iodine compounds are recovered from the gland is given and the conclusion is reached that approximately half of the iodine is present as thyroxine and half as diiodotyrosine—the latter being an intermediary in the biological synthesis of thyroxine. Chapter v shows modestly how the constitution of thyroxine and its synthesis were established, these being the author's own achievements. Chapter vi deals with the biological methods of measuring thyroid activity. Chapter vii studies the relation of thyroxine to total thyroid activity and is of great interest. Thyroxine is the only physiologically active constituent of the thyroid. Glandular activity consists in the following sequence of events: (*a*) Iodination of tyrosine; (*b*) Synthesis of thyroxine; (*c*) Production of colloid for storage; (*d*) Release of active secretion. The first of these depends on the supply of iodine; the last on the demands of the organism.

In the last chapter the author briefly discusses Graves' disease. He regards this as a condition in which the thyroid delivers an abnormal amount of normal secretion—a diarrhoea of the thyroid. The cause of the excess liberation is to be sought outside the thyroid.

An appendix sets out the methods of estimating iodine in organic substances.

The Anatomy of the Human Skeleton. 3rd ed. By J. Ernest Frazer, D.Sc. (London), F.R.C.S. (Eng.), Professor of Anatomy in the University of London and Lecturer in the Medical School of St Mary's Hospital. (London: J. and A. Churchill.) 1933. Pp. viii + 292 with 219 illustrations, many in colour. Price 28*s.* net.

The third edition of this well-known work has now been published. It is a monument to the industry, the learning and the artistic skill of the author. In no other book has an anatomist ever succeeded in extracting so much information about the structure of the human body by reference to what can be seen and felt on bones as is to be found in *The Anatomy of the Human Skeleton*. The illustrations, the work of the author himself, presented to elucidate the conception of the book form a unique series.

The preface contains a humorous reference to the relativity of truth, this being conditioned by the limitations of one's own environment. The remark arises out of the impossibility of being more than approximate in the date of the appearance of centres of ossification. The author states that he has attempted to give a reasonably reliable account of this matter—within his environment. It is to be hoped that the students who meet him at examinations will not attempt to hoist him on his own petard, and claim acceptance of their statements on the ground that within the limits of their environment they are reasonably reliable.

The Main Afferent Fiber Systems of the Cerebral Cortex in Primates. By Stephen Poliak, M.D., Associate Professor of Neurology, Department of Medicine, University of Chicago. (University of California Publications in Anatomy, Vol. ii. University of California Press, Berkeley, U.S.A.) 1932. Pp. xiv + 370. 96 figs. in text. Price $10.00.

This monograph presents in very great detail the author's investigations of the somatic sensory, the auditory, and the visual pathways of the cerebral cortex based upon the degenerations produced by experimental lesions in monkeys and studied by

the Marchi method. He has concerned himself with the problem of their localisation in the subcortical centres, the arrangement of the afferent fibres in the radiations, the precise limits of the cortical areas which the radiations reach and the finer connections of the terminal fibres within the cortical laminae.

In this work Dr Poliak has gone over ground which of course has been frequently studied before. He has set himself the task of emphasising the strict anatomical localisation of the radiations he has studied and tried to achieve the greatest precision in his topographical results. The earlier literature is discussed fully and fairly and where discrepancies occur with the earlier work he has attempted to explain how such have arisen.

It is perfectly clear that the strictest anatomical localisation does occur in these spatially discriminative sensibilities and of these it is most perfectly established in the case of the visual pathway. Whether this is due to the physiological qualities of vision or whether it arises from the greater ease with which precise experiments can be performed on the visual pathway is not quite certain. At any rate this point to point correspondence of the peripheral receptor field, the subcortical centres, and the area of cortical termination are most impressive in the case of vision. It seems that a similar state of affairs exists in the case of the other two afferent pathways studied but the experimental demonstration has not yet been so convincingly achieved.

Dr Poliak proceeds further to state the implications of this anatomical precision in localisation and presents the issue between the localised performance of function by limited areas of the cerebral cortex as opposed to the very common acceptation by physiologists and perhaps psychologists of the dynamic equipotentiality of all parts of the cortex. The localising view has now a great deal of anatomical and other evidence behind it. A decision between these two theories is of great importance at the moment for upon the conclusion reached the planning of all future cerebral research depends. These are matters which Dr Poliak discusses and his anatomical results at the moment incline him strongly to range himself amongst the localisers. He rightly points out that so much of cerebral physiology is crude and inexact because the knowledge is not yet available by means of which it could be decided what elements in behaviour and sensation it is right to expect to be localised.

Altogether the monograph is of great interest reflecting no less on the author's ability to plan, execute, and interpret experiments than upon his skill in perceiving and discussing the larger issues involved.

Repetitorium anatomicum. Von BROESIKE-MAIR. 3rd Auflage. (Leipzig: Fischers med. Buchhandlung.) 1932. Pp. x + 305. 71 Text-figs. and 1 Plate. Price M. 18.

This book originally written by Dr Broesike has now been published as a third edition under the authorship of Dr Mair. As the title indicates it is the intention that the book should serve as a means by which the student can quickly revise his knowledge of the more important anatomical facts. The book comprises a text of 279 pages with 71 illustrations many of which are in colour.

The treatment of anatomy is by systems and the largest amount of space is devoted to the bones, muscles, joints and ligaments. Of necessity the information given in such a small compass must be brief but often it amounts to little more than the name of the structure or organ. However, the fact that it is now in its third edition suggests that German medical students find it useful.

Anatomical Society of Great Britain and Ireland

PROCEEDINGS

November, 1932 *February*, 1933
May, 1933 *June*, 1933

RECORDED BY
R. J. GLADSTONE

EDITED BY
E. BARCLAY-SMITH

PROCEEDINGS OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND

NOVEMBER, 1932

The Annual Meeting of the Anatomical Society was held at St Bartholomew's Hospital Medical College on 25 November, 1932.

The Chair was first taken by Professor LUCAS KEENE, and subsequently by the President, Professor WRIGHT.

Dr R. E. NORRISH and Professor H. H. WOOLLARD made a communication on the "Relative frequency of the vaso-motor nerves in the different parts of the extremities," which will be published in the *Journal of Anatomy*.

Dr R. PAINE read a paper on the "Anatomy of the salivary glands as revealed by lipiodal injections in the living."

Dr F. DAVIES enquired whether a duct of Bartholin was present or not, and what was the drainage of the sublingual gland.

Dr PAINE replied that there was no indication of a duct of Bartholin in the specimens examined.

Mr F. H. AITKEN WALKER read a paper on the "Blood supply and lymphatic drainage of the thyroid gland," illustrated by lantern slides, drawings, and specimens.

An erroneous description of the relative distribution of the thyroid arteries, which has been accepted by many writers without question, may be stated as follows: "The superior artery supplies mainly the connective tissue and capsule of the gland. The inferior artery supplies the parenchyma or gland substance proper." This statement is incorrect.

There is a very free extraglandular anastomosis between the two superior arteries, and between the superior and inferior arteries of the same side. This can be shown by dissection or any simple vascular injection. In this investigation injections were made of one or more thyroid arteries, either separately or simultaneously with coloured gelatine solutions and/or a suspension of barium, and examined by stereoscopic skiagram or cleared section.

There is no intraglandular anastomosis; each artery supplies a well-defined area of gland parenchyma. The superior artery supplies the superior pole, anterior part of the lateral lobe, and the anterior and superior part of the isthmus. The inferior artery supplies the inferior pole, posterior part of the lateral lobe, and a variable amount of the posterior part of the isthmus.

There is no particular arrangement of the branches of an artery to the lobules of the gland. One lobule may receive many separate arterioles, and along the line of demarcation a lobule receives branches from both superior and inferior arteries.

The capillary network around the follicle showed that it received a supply from two or more arterioles, and along the line of demarcation a single follicle received a supply from both superior and inferior arteries.

The lymphatics of the gland were shown to start as a network of lymph channels surrounding the follicles with their capillaries. These are collected into a subcapsular network from which lymphatics drained along the course of the thyroid veins into the deep cervical chain of glands. This confirms the clear and detailed descriptions which appear in the monographs on this subject.

The post-mortem material used prevented any observations on the direct communications between lymphatics and the great veins.

Professor WOOLLARD said that there is no doubt that the superior thyroid artery supplies the parenchyma of the gland as well as the connective tissue and capsule.

The PRESIDENT enquired whether the lymphatic vessels opened directly into the veins without the intervention of lymphatic glands, or not.

Mr WALKER replied that he believed the lymphatic vessels usually traversed the deep cervical glands before opening into the veins, but he had been unable to make any direct observations on this point.

Mr DE BEER read a paper entitled "The development of the skull in birds," illustrated by drawings projected from the epidiascope, and by preparations of whole mounts exhibited under the microscope. He stated that the object of his paper was not so much to report on a definite piece of research, as to draw attention to the methods by which the problems connected with the development of the skull in Vertebrates may most profitably be attacked. The method of reconstructing skulls from serial sections by means of plates of wax (or, better still, blotting-paper soaked in wax) has been in vogue for over half a century, and is, of course, very valuable. Not only does it supply permanent objects for study and comparison, but it enables the morphological relations of neighbouring structures (blood vessels, nerves, etc.) to be accurately defined. It suffers, however, from the fact that it is extremely laborious, which means in practice that in the study of the development of any form the investigator has to content himself with reconstructed models of a few stages only, with serious gaps in between.

But another method for the study of the chondrocranium has been in use for over a quarter of a century, namely the van Wijhe technique for selective staining and clearing of whole embryos. By this means the developmental modifications of the skull can be followed, not merely in a few stages, but in hundreds, and consequently a continuous series without gaps becomes available for study. It is surprising that this method should not have found a wider application. Its only disadvantage is that it reveals the skeletal elements only, and not the neighbouring structures, the relations of which are all important for the identification of the skeletal elements. But this difficulty may be readily overcome by referring to a reconstructed model.

The ideal method of studying the development of a chondrocranium, therefore, is to prepare as many specimens by the van Wijhe technique as possible, and to make quite a small number (say two) of reconstructed models. For the study of the osteocranium, the same principle may be followed by substituting the alizarine technique for bone for the van Wijhe technique for cartilage.

Mr DE BEER proceeded to illustrate some of the points raised by reference to his study of the development of the chondrocranium of the duck. In the first place he showed how closely the morphological changes could be followed step by step, and in particular he demonstrated how it comes to pass that the

maxillary and mandibular branches of the trigeminal nerve become separated from the profundus branch, by a fusion of cartilages in between. Next, he illustrated the importance of not relying solely on the one or the other method, by showing that the structure which in Birds was previously taken to be the lamina orbito-nasalis, is in fact the orbital cartilage, as evidenced by the relations to it of certain nerves. Lastly, he showed how a close series of stages, and the possibility of contemplating the whole skull together with the vertebrae, enabled the suggestion to be made that the curious and puzzling cartilage which in Birds forms the floor of the tympanic cavity was originally derived from one or more cranial ribs.

In conclusion, Mr DE BEER appealed for human material in order that the outstanding problems in the development of Man's chondrocranium might be cleared up.

Professor J. P. HILL congratulated Mr DE BEER on his beautiful demonstration of the development of the chondrocranium in Birds. The early stages showed a relatively primitive type of the occipital region. The methylene-blue method shows remarkably well the presence of additional cartilages to those which were previously known.

The PRESIDENT asked whether the occipital region was represented by four or five segments fused on to the skull.

Mr DE BEER replied that the number of segments incorporated in the skull varied in different types, more particularly in the Selachia.

REFERENCES

(1) Methods for demonstrating cartilage in whole preparations:
van Wijhe, J. W. *Konink. Akad. v. Wetensch. Amsterdam*, Proc. of Sat. May 31, 1902; p. 47.
van Wijhe, J. W. *Bijdragen tot de Dierkunde*, 1922, vol. XXII, p. 271.
(2) Methods for demonstrating bone in whole preparations:
Gray, P. *Museums Journal*, 1929, vol. XXVIII, p. 341.

Professor J. SHELLSHEAR made the following communications:

(*a*) (For Dr RUBINO) "The arterial supply of the cerebral cortex."

(*b*) "Marshall's Bushwoman's brain."

Dr WILFRED SHAW exhibited sections and lantern slides of two early human ova:

(1) A chorionic vesicle surrounded by decidua and enclosing an embryonic rudiment, which consisted of amnion, yolk sac and embryonic plate, and measured 1·66 by 1·4 by 1 mm. It belonged to group E of Bryce's classification, and the plate showed a cloacal membrane, primitive streak and groove, Hensen's node, a blastoporal opening with a well-marked dorsal lip, and a commencing chordal plate.

The specimen was removed from a woman aged 32 on whom Dr SHAW had performed a subtotal hysterectomy for a myoma. The left ovary contained a corpus luteum.

The following dates were obtained:

(1) From the day of insemination 26 days.

(2) From the day of menstruation expected by the patient 7 days.

(3) From the calculated onset of menstruation 10 days.

(4) From the date of onset of the last menstrual period 38 days.

Dr SHAW discussed the relation of fertilisation to ovulation and insemination. He considered that ovulation was usually restricted to the interval between the 13th and 16th days of the menstrual cycle, and pointed out that insemination before the date of ovulation was not necessarily sterile, since spermatozoa may survive for a considerable period in the female genital tract. In the case under consideration insemination corresponded to the 12th day of the menstrual cycle, or two days before the expected time of ovulation.

The general features of the specimen may be summarised under the following headings:

Trophoblast: Chorionic villi are more plentiful at the circumference of the flattened blastocyst than beneath the operculum or adjacent to the decidua basalis. They show a minor degree of branching, but most of them are single and are not vascularised. A basal layer of chorionic epithelium is present (cyto-trophoblast) and masses of plasmodi-trophoblast which are so abundant that the total volume of this tissue is as great as that of the whole of the chorionic villi. The cells of the plasmodi-trophoblast are large and vacuolated.

Decidua: The decidual glands are hypertrophied, crenated and filled with a pink (eosin) staining coagulum. The gland cells are high columnar and contain globules of secretion. The ovum lies imbedded in the compact layer and the decidua capsularis is well defined. Most of the decidua which surround the ovum contain areas of necrotic tissue. Here the glands are disintegrated, decidual cells are degenerate, and there is much nuclear debris, interstitial hæmorrhage and leucocytic infiltration. Large areas of trophoblast are adherent to the inner surface of the decidua. There is little maternal blood in the space between the chorionic villi and the decidua, but large maternal blood sinuses are present in the decidua in the immediate vicinity of the ovum.

The ovum: The chorionic epithelium is lined by a thin, indefinite layer of extra-embryonic mesoderm which is continuous with the single layer of cells surrounding the amnion and yolk sac. Elsewhere the primitive reticular tissue has disappeared and been replaced by coagulated material.

No trace was found of a yolk-sac duct connection with the chorion, nor were there any remains of an extra-embryonic cœlom. The connecting stalk attaches the embryo to the chorionic epithelium and is made up of round cells with spherical nuclei which are quite different from those of the extra-embryonic mesoderm. Unlike the amnion and the yolk sac, the connecting stalk has no covering layer of extra-embryonic mesoderm, but its rounded cells merge with those of the extra-embryonic mesoderm at the periphery near the chorionic epithelium. The connecting stalk contains the amniotic duct, allantois and blood vessels. The allantois measures 0·33 mm. in length, is lined by high columnar epithelium, and is a tubular prolongation from the caudal end of the yolk sac into the connecting stalk. The allantois is surrounded by allantoic blood vessels which pass further into the body stalk than does the allantois. They contain no blood cells, and are less conspicuous than the blood islands of the yolk sac. Vessels similar to those of the allantois are found in the extra-embryonic mesoderm beneath the chorionic epithelium in the region of the connecting stalk, but it was found impossible to trace a communication between the two systems. A large and well-defined blood island was identified on the wall of the yolk sac near the origin of the allantois. Already therefore the mechanism by means of which the foetal vessels form the umbilical vessels and pass to the chorion has been initiated.

The amnion is roughly circular in shape, measuring 1·35 by 1·34 mm. in area and 0·32 mm. in height. It is longer than the yolk sac, since it extends caudally to form a primitive caudal fold. On the other hand the yolk sac extends further forward than the amnion by 0·09 mm.

The yolk sac measures 1·21 mm. in length, 1·35 mm. wide and 0·4 mm. in height. The yolk sac is lined by entodermal cells, which are flattened over the greater part of its extent, but in the vicinity of the allantois the cells become columnar. Similar columnar cells are found in a small area of the yolk sac, which perhaps corresponds to the site of the connecting strand of the Bryce-MacIntyre ovum, but which is not represented in this specimen. In its caudal part the yolk sac is surrounded by a single layer of extra-embryonic mesoderm, so that two layers of cells, the extra-embryonic mesoderm and entoderm, form the wall. Near the middle of the embryo blood islands are found between these two layers. They contain large polygonal cells, some of which have cell-bodies deeply stained with eosin. The nuclei are large and show active mitoses. The endothelial lining of the blood islands is incomplete.

Embryonic plate: The cloacal membrane and the blastopore are on the amniotic side of the plate. The cloacal membrane lies at the caudal end of the primitive streak and is seen best where the allantois arises from the yolk sac. It measures 0·09 mm. in length and along the cloacal membrane the ectoderm and entoderm fuse. The primitive streak measures 0·43 mm. in length. Cranially the streak ends at Hensen's knot. The knot measures 0·04 mm. in length: in front of it lies the blastopore opening and chorda canal. The latter can be traced downwards and forwards towards the entoderm. It was not possible to trace a communication of the chorda canal with the entodermal cavity, although the direction of the canal and the arrangement of cells around it were very suggestive that such communication existed. Cranial to the blastopore, a neural plate is being formed, but there are no neural folds.

The embryonic mesoderm differs in type from the extra-embryonic mesoderm. It forms lateral sheets which lie on either side between the entoderm and ectoderm, and which arise mainly from the cells of the primitive streak.

Dr Wilfred Shaw also showed an example of Omphalopagus parasiticus. The specimen was removed by Dr Malcolm Donaldson by an abdominal hysterectomy. The patient was suffering from morbus cordis, and when she was examined during the first few weeks of her pregnancy was found to have a fimbrial cyst. The operation was performed 44 days after the onset of the last menstrual period. The specimen consisted of two embryos joined in the umbilical region. The embryos differed in size. The larger of the two was 3·15 mm. in length, and 1·46 mm. in width. It appeared to be normally developed except along the line of fusion. The smaller embryo was incomplete, consisting only of the caudal part below the level of the umbilicus, there being no head, heart or liver. The monster had a single chorion and amnion and only one umbilical cord. The axes of the two embryos were parallel. In the parasitic embryo there was no evidence of lower limb buds. The neural tube, notochord, mesonephros, mesentery and intestine are normally developed from the part of the embryo which is represented in the specimen. The neural tube ends blindly in the cranial part of the embryo and is closed. Six somites can be counted in the specimen and they correspond in development with those of the larger embryo. The intestine also ends blindly when traced cranially, but

there is a suggestion of division in its upper part which recalls the lung buds of the larger embryo. The vascular system is represented by a single dorsal aorta and cardinal veins.

The vascular system of the larger embryo was normally developed. It was found difficult to trace any vascular connections between the two embryos, and it appears unlikely that the parasitic foetus would have been vascularised from the host during extra-uterine life except by way of umbilical vessels.

Dr SHAW discussed the problem of origin of double monsters, and pointed out the difficulties in accepting the hypothesis that the two embryos are derived from the two parts of the first blastomere division of the fertilised ovum. The blastomere hypothesis necessitates the assumption that each embryo possesses its own trophoblast, but in the specimen under consideration there was a common chorion, amnion and umbilical cord, and there was no evidence of fusion of either trophoblast or amnion.

The PRESIDENT congratulated Dr SHAW on his demonstration of two very interesting specimens, and remarked, with reference to the second specimen, that the mode of origin seemed to be most satisfactorily explained, by assuming that a splitting of the posterior portion of the embryonic axis had taken place.

Dr R. G. CANTI showed a cinema film illustrating the growth of tissue cultures from embryonic explants supplied by Dr Honor Fell. The preparations had to be kept sterile and were cultivated in plasma and embryonic extract. Some of the preparations were taken from chick-embryos.

He also showed specimens illustrating segmentation of the rabbit's ovum.

Professor HILL congratulated Dr Canti on his very beautiful demonstration and remarked that such films should be used in every laboratory where Embryology is taught; he considered them to be a valuable addition to the ordinary methods of teaching.

Dr J. M. YOFFEY read a paper on "Observations upon cultures of lymphoid tissue," which will be published *in extenso*.

Professor W. E. LE GROS CLARK with Dr R. H. BOGGON made a communication on the "Connections of the anterior nucleus of the thalamus," which will be submitted for publication in the *Journal of Anatomy*.

Professor F. KISS (Hungary) read a paper on the "Comparative anatomy of the spinal ganglia." The author examined by his prolonged osmic acid method (*J. Anat.* vol. LXVI, 1932) the spinal ganglia of the Vertebrates. He demonstrated spinal ganglia of various Mammals, Birds, Reptiles, Amphibia and Fishes. He found two types of cells in the spinal ganglia. Type I is a round (large or small in size) pale cell. Type II is a multipolar, dark cell. Cells of Type I are usually in the majority, while those of Type II are scattered amongst the cells of Type I. He found very few of Type II in the white rat and none of this type in the frog. He concluded on the basis of his morphological and experimental work that Type I represents the sensory, Type II the autonomic (sympathetic) cells of the spinal ganglia. Spinal ganglia of different species and of different segments of the same animal vary in the relative number of the two types, but the dark, multipolar cells are constant physiological elements of the spinal ganglia. The dark, multipolar cells are in Man mostly on the periphery of the ganglion and in obvious minority.

The form, size and coloration of the pale (sensory) cells change with age. Thus the distinction between the two types is not so marked as in earlier life.

Experimental work on cats (in collaboration with M. L. O'Shaughnessy, Royal College of Surgeons, London) shows that after section of certain branches of the cranial and spinal ganglia the dark coloration of the multipolar cells disappears.

The following took part in the subsequent discussion:

Dr STIBBE asked if the multipolar, dark cells described were the same as the small spinal ganglionic cells of the previous literature or altogether different from them.

The PRESIDENT asked if the relative number of the two types varied in the different segments of the same individual.

Professor BLAIR observed that it had been possible to demonstrate the two distinct types of cell in the heart of the guinea-pig by using the osmic acid method and also by means of a silver stain.

Professor BRASH asked which of the two types of cell was affected by age.

Professor WOOLLARD said that in his view only one type of cell had been demonstrated; the different appearance he attributed to deficient fixation.

Professor HILL observed that in his opinion the nerve cells projected were in an excellent state of preservation. Their appearance showed evidence of a most careful technique.

Professor KISS stated in reply that although he recognised that the pale staining cells were of two types, one larger than the other, in his opinion the multipolar dark cells demonstrated were a third distinct type. The morphology of these small dark cells was identical with that of sympathetic ganglion cells. Work is in progress to decide the segmental distribution of the small dark cells. It has been found possible to identify the two types of cell by other staining methods (Toluidin) as well as by the use of osmic acid. Age effects seem most pronounced in the large pale cells. In this connection most careful technique is essential, and the absence of shrinkage or other artificial changes in the cells projected is evidence that such technique was employed.

A paper by Professor S. SHEA on "Diaphragmatic hermia" was communicated by the SECRETARY.

FEBRUARY, 1933

An ordinary meeting of the Society was held at the Middlesex Hospital Medical School on Friday, 3 February, 1933. The President, Professor W. WRIGHT, in the chair.

Professor J. CAMERON read a paper on "The humeri of the ancient slingers of Minorca."

Professor FRAZER alluded to a facet on the summit of the neck of the humerus which was produced by the pressure of the capsule of the shoulder-joint, and the prominence of the deltoid tubercle which was present in muscular subjects.

Professor MEEK enquired whether there was any sex difference in the degree of prominence of the deltoid eminence.

Professor SHELLSHEAR mentioned that the women in China have no prominent ridges on their humeri, although the coolie women lift heavy weights and do manual labour.

Dr A. A. ABBIE read a paper on the "Choroidal arteries," which will be submitted for publication in the *Journal of Anatomy*.

Professor WOOLLARD commented on the functional and homologous relations which existed between the dorsal and ventral nuclei of the thalamus with reference to their blood supply.

Professor LE GROS CLARK remarked that there was still much to be demonstrated with regard to the arterial supply, in spite of the work done by Beevor and others. The macular area was supplied by both arteries. In the lemur there are six layers of cell laminae, and he considered that the study of the vascular supply of this region would be facilitated by the use of longitudinal as well as transverse sections. In the primitive lemur a ventral nucleus is present as well as dorsal nuclei. The ventral nucleus has the same blood supply as the subthalamus. He expressed the hope that Dr Abbie would continue his researches.

Professor HARRIS referred to the association of the blood supply of particular areas of the brain with certain functions which had been suggested by Dr Abbie's demonstration, and said that it had its counterpart in Hilton's Law, namely: "A particular function is subserved with blood supply of a particular artery."

The PRESIDENT said that Dr Abbie's work afforded an excellent illustration of the way in which the structure of the central nervous system can be unravelled by a study of its blood supply, in the same way as muscles by their nerve supply. He commented also on the name "choroidal" which gave the impression of the distribution of these arteries being solely to the plexuses of the ventricles.

Dr C. G. PAYTON read a paper on "The growth of the epiphyses in the long bones in the madder-fed pig," which will be submitted for publication in the *Journal of Anatomy*.

Professor H. A. HARRIS pointed out that there was no histological nor radiographic evidence for any process of absorption of epiphysial bone in the zone immediately adjoining the epiphysial cartilage. If the process of bony absorption were common in this area then some measure of osteoclastic activity would be seen thereat in histological section.

The PRESIDENT remarked that orthopaedic surgeons maintain that so-called separation of epiphyses were in reality fractures on the diaphysial side of the epiphyses, which seemed to indicate the existence of a weak line in this situation.

Dr PAYTON, in reply to Dr Harris, said that he was not acquainted with the appearance of concentric lines in growing epiphyses, but he had seen divergent lines. With regard to the difference between the expected and the actual growth of bones, and the bearing that this has on the question of absorption of bone, he believed that his deductions were essentially correct, and at any rate not to be explained away entirely.

In reply to the remarks made by the President he stated that fractures produced experimentally passed through the diaphysis on the diaphysial side of the epiphysis.

Mr RALPH THOMPSON said that fractures took place through the diaphysis, but epiphyses could be separated. If congenital syphilis was present, separation of the epiphysis could occur.

Dr A. L. P. JEFFERY showed "An unusual congenital deformity of the heart." The interventricular septum appeared to be absent and there was an alteration in the relative positions of the aorta and pulmonary artery. Dr JEFFERY believed that in normal development the interventricular septum rotates passively, the twist being most probably determined by alterations in pressure of the blood stream in the ventricle.

Professor FRAZER did not agree with the statement of an absence of the interventricular septum, and said that the "pulmonary artery" had all the appearance of an aortic arch. Abnormalities usually appeared in the aortic part of the organ, or common arterial sinus.

Mr A. R. THOMPSON, Mr W. J. FERGUSON, and Mr J. A. W. MILLER made a joint communication on "Some congenital deformities of the kidneys." Mr THOMPSON showed two cases of so-called "solitary kidney." (1) One kidney was very large, the other was represented by a mere tag attached to the upper end of the ureter. (2) A case in which the left kidney was four times the size of the right. He mentioned also a third case of "solitary kidney" which was removed! It was much longer than usual.

He also showed specimens of horse-shoe kidney and drew attention to the importance of noting the position of the vessels supplying the organ, and of the ureters. Some cases of "solitary kidney" were in reality "horse-shoe" kidneys which had been rotated to one side, as in a female subject in which the rotation was to the left. Two ureters were present issuing from the anterior aspect of the organ, and passing down to end separately in the bladder. He showed also a horse-shoe kidney with a fibrous bridge at the lower end uniting the two parts. He considered the fibrous bridge to be an acquired condition not congenital. He further showed a photograph of a left ureter which exhibited opacities. These he believed to be prostrate stones which had migrated upward. He alluded to cases of twisted and double ureters, and said that double ureters are liable to give rise to symptoms, the capacity of the pelves of a double ureter being less than that of a single normal pelvis.

The PRESIDENT mentioned a case of a double kidney in which one kidney was enclosed within the other, and alluded to cases in which a suprarenal body was found enclosed within the kidney.

Professor FRAZER agreed with Mr Thompson's statement that some cases described as "single kidney" were in reality "horse-shoe." The kidneys were at first fixed in the sacral region and may remain in the pelvis; occasionally one passes up into the abdomen, while the other retains a pelvic position.

Professor LE GROS CLARK and Dr R. H. BOGGON made a communication on the "Connections of the medial nuclei of the thalamus in the cat," which will be published in the *Journal of Anatomy*.

Dr A. J. E. CAVE made the following two communications:

(1) *A note on the vertebral artery.* The loop of the atlanto-axial segment of the vertebral artery is determined by that vessel's immediate relations. Medially lie the articular masses of the first two vertebrae, laterally are the

splenius and levator anguli scapulae muscles (longissimus cervicis and complexus have no attachments above the axis). The splenius and levator muscles are separated from the vessel by a quantity of venous fibro-fatty tissue. The bend is therefore antero-posterior with a forward concavity; the degree of tortuosity may vary with age. Much fatty areolar tissue surrounds this segment of the artery, and in this the anterior primary division of the second cervical nerve maintains a very close relationship to the vessel being successively behind, lateral to and then anterior to the artery, finally appearing medial to the inner margin of the first (atlantal) slip of scalenus medius through the vascular fat in front of the atlanto-axial capsule: thence the nerve turns laterally across the medius into the first loop of the cervical plexus. The numerous small veins which abound in the fatty areolar tissue of this region are tributaries of the vertebral, deep cervical and descending cervical veins.

(2) *A microcephalic cranium.* The specimen (Leeds Path. Mus. No. 7865) is the cranium of a former workhouse inmate, a male of 52. The anterior half is detachable, and of the teeth present at death only the left (maxillary) canine remains *in situ*. There is no history beyond the statement that the patient had "the intelligence of a dog," and that the brain (not preserved) weighed at autopsy but 16 oz. A sister, 4 ft. 8 in. high, was similarly affected.

The cranial capacity by the millet seed method is approximately 380 cc., and even with the most generous allowance for error is still well below 400 cc. The cranium yields the following data:

	mm.		
Max. length (glabella-inion) ...	120·2	Cephalic index ...	77·6 (mesaticephalic)
Max. width (biparietal) ...	93·3	Cephalic height index	79 (hypsicephalic)
Bimastoid width	95·5	Gnathic index ...	101 (mesognathous)
Basi-bregmatic height	95	Facial index ...	58·6 (leptoprosope)
Bizygomatic width	c. 93	Orbital index ...	97 (megaseme)
Basi-prosthion	80	Nasal index ...	49 (mesorhine)
Basi-nasion	79		
Nasion-prosthion	54·5		

The hypoglossal canals are relatively large, the right being subdivided; the posterior condylar foramina are large relatively and absolutely; the optic foramina are capacious, the sphenoidal fissures short and wide; there is a right carotico-clinoid foramen. Most of the sutures remain open, including the coronal; the hinder third of the sagittal and the anterior part of the lambdoid sutures are in process of obliteration. The cranial base shows traces of the exoccipital elements, with a left-sided abortive attempt at a paramastoid process. There is presumptive evidence of righthandedness in the greater development of the left occipital polar fossa. Although the whole cranium manifests a general reduction of all parts as compared with the normal it would appear that such reduction affected principally the frontal and parietal regions, but a precise picture of the brain itself remains to be revealed by an endocranial cast.

Professor SHELLSHEAR in commenting upon the cranium said that it represented one of two forms met with in this condition, and offered to obtain an endocranial cast of the specimen.

Professor R. D. LOCKHART communicated "A further note on movements of the shoulder-joint." Descriptions of shoulder-joint movements must start from an initial position with the subject standing erect, the arm dependent,

and the palm of the hand directed forwards, that is, the elementary position which is an axiomatic postulation in all anatomical descriptions, otherwise the meaning of the various writers becomes obscure.

Radiograms of the shoulder-joint with the arm raised erect by flexion (or advanced abduction), and by abduction from the elementary position, were shown, to demonstrate the fact that the terminal position of the structures, irrespective of the plane traversed in gaining the erect attitude, is certainly not the same (1). Raised by flexion, the palm is directed backwards, and the great tuberosity of the humerus mainly laterally. Raised by abduction, the palm is directed forwards, and the tuberosity mainly medially. When the living subject is examined under the radiographic screen, with the arm held erect, the humeral head can rotate exceptionally freely, almost like a whirligig. It is important to examine several subjects, because the movement is remarkably restricted in certain individuals. The statement (1) that the arm cannot be abducted into the erect position without lateral rotation of the humerus occurring, entirely depends upon the position from which elevation occurs. Certainly, if the palm is directed medially in the dependent position, and also medially in the erect position, then external rotation does occur, but is not necessary in elevation by abduction from the postulated initial position.

In a previous publication (2), the statement, that the terminal position of the structures in the elevated arm is necessarily the same, was made relative to the amount of humeral articular surface escaping from the glenoid cavity, and is contextually accurate.

Exception was taken to the statement in leading texts (3) that abduction of the arm in the plane of the scapula, or plane of pure abduction, is a more simple movement than by any other plane of elevation, and that this plane allows the humerus to derive full benefit from the rotating scapula. In the publication already referred to (2), it was found that when the arm is abducted from the body to any angle whatsoever, and the limb swung to and fro, so that all possible planes are traversed, the position of the scapula is practically the same in every one of them, except that the further forwards the arm is swung the more apparent is a slight winging of the vertebral border, although the inferior angle remains applied to the thoracic wall. In other words, there is pivoting of the scapula upon its inferior angle to the backward and forward movement of the arm. In fact, it is questionable whether the arm can be raised in any plane that is not also the plane of the scapula (4). The marked tapering of the upper thoracic wall to the neck is important in this connection.

The point was emphasised that there is great variation in the details of movements of many individuals, for example, heavy weight lifters, acrobats, tennis and badminton players.

Reference was made to the erroneous inference which may be drawn from the teaching tradition that, if the muscles are dissected from the shoulder-joint and the capsule punctured, the bones will separate for 2 or 3 cm. The fact is that the muscles of the greater part of the capsule can be removed, but, provided the upper part of the capsule is left intact, no amount of force will separate the bones until abduction is secured. It is this upper part of the capsule which suspends the head in such a way that the lower border of the anatomical neck of the humerus rests one-third of the way up the glenoid cavity when the arm is in the dependent position.

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MAY, 1933

An ordinary meeting of the Society was held in the Institute of Anatomy, University College on 5 May, 1933. The President, Professor WRIGHT, in the Chair.

Dr A. J. E. CAVE read a paper on the "Dorsum sellae." From the viewpoints of both topography and morphology great interest attaches to the uppermost portion of the dorsum sellae of the sphenoid, i.e. to the transverse bar which bears at its lateral extremities the posterior clinoid processes. This interclinoid portion, sometimes smooth, at other times exhibiting curious osseous "candle-gutterings," has commonly an obvious independence of the rest of the bone, a point usually omitted from the text-book accounts of sphenoidal variations and seemingly mentioned by only one such work (Buchanan's *Anatomy*, 6th ed. 1925).

Examination of a large series of crania (both fresh and dried) reveals positive or suggestive evidence of such independence in 70 per cent. cases, whilst in the remaining 30 per cent. only, does the official type of dorsum occur, i.e. a dorsum wherein the clivus Blumenbachii continues without interruption to its superior extremity. Of the 70 per cent. cases mentioned, 50 per cent. exhibit a groove or constriction demarcating the interclinoid portion from the remainder of the bone (as noted by L. Calori, *Mem. d'Accad. d. Sc. d. Bologna*, 1892) whilst in the remaining 20 per cent. the interclinoid is free and is connected to the sphenoid proper by suture (as recorded by W. Gruber, *Abhand. a. d. Mensch. u. vergl. anat.* St Petersburg, 1852) or by synchondrosis. Although Calori (*op. cit. supra*) records separate centres of ossification for the posterior clinoid processes themselves as occurring in subjects of 10–11 years, yet it seems that ossification of the interclinoid element is synchronous with that in the rest of the post-sphenoid, and, further, that neither age nor sex appears to determine what particular type of dorsum shall prevail in any given case.

This independence of the interclinoid has not escaped previous observation and comment, although nowhere in the scanty literature of the subject is any explanation tendered as to the underlying reason for this curious independence. The explanation may depend upon morphological or upon purely mechanical local factors, as discussed below. P. Albrecht (*Biol. Centralbl.* 1885) was familiar with this condition, and demonstrated the separate nature of the interclinoid in the foetal antelope, young baboon and monkey; he named the interclinoid element the "basiepisphenoid," and the lower portion of the post-sphenoid the "basiorthosphenoid." Calori noted these two parts united by synchondrosis in children. Staurenghi (*Bollet. d. Soc. med. chir. d. Pavia*, 1899) recorded the occurrence of multiple centres of ossification in the bovine

dorsum sellae, a condition which Le Double (*Variations des Os du Crane*, Paris, 1903) believes may obtain in the human subject, although he cites no specific examples.

Personal research upon anthropoid and primate material had demonstrated that in these forms the typical configuration of the interclinoid element is that of a bony transverse bar bearing the (usually small or rudimentary) posterior clinoid processes and sending downwards from either end a footpiece which meets the rest of the post-sphenoid; the whole element having thus the shape of a capital E with the centre bar removed and laid sideways. Again interclinoid independence is manifest in the great majority of cases; union between parts is generally by either suture or synchondrosis, although examples of synostosis also occur. A gap or fenestration is commonly visible between the two parts of the dorsum, though such may occur wholly within the interclinoid portion, and rarely, a double window is found. This gap, occasional only in man, has been noticed not only in primates generally but also in carnivora and in ungulates (F. Frassetto, *Anat. Anz.* 1901). Gruber's petro-sphenoid ligament is usually attached, as in man, to the post-sphenoid proper. The lateral tips of the interclinoid are occupied by the attached border of the tentorium, occasionally showing spicular lateral projections which are ossifications of or into that structure.

In man the interclinoid portion of the bone exhibits most frequently a median groove or sulcus for the pituitary stalk, and lateral thereto on each side a fainter groove or impression for the posterior communicating artery of the circle of Willis. Should a lateral spicule project from the posterior clinoid process itself such spicule underlies the oculo-motor nerve. The optic tract or even the optic chiasma may lie above, though out of actual contact with, the interclinoid bar. Gruber's ligament presents variations of attachment, being most often fastened to the post-sphenoid proper but sometimes to the region of the posterior clinoid process. Whatever its particular type the whole of the posterior aspect of the entire dorsum is firmly clothed by endocranial dura.

As to the actual morphological nature of the interclinoid or basiepisphenoid, the possibility of its being a traction epiphysis closely connected with the mechanical pull of the tentorium readily occurs to mind. It seems possible that the changes in orientation of the sphenoidal dorsum, the tentorium and the petrous temporal, consequent upon cerebral enlargement and therefore altered cranial configuration, have some ontogenetic influence in determining instability of this element. Yet against this ready likelihood must be considered the following facts:

(*a*) An independent interclinoid occurs in sub-human forms with great frequency, and herein, obviously, specifically human factors cannot be causative. (*b*) Of the attached tentorial border, but a very small portion is fastened to the posterior clinoids, the greater extent being fixed to the rigid cranial wall, and it is difficult to visualise any degree of active traction under these conditions. (*c*) Traction by Gruber's ligament is equally out of the question because of the inconstancy of its sphenoidal attachment, which is generally to the main mass of the post-sphenoid. (*d*) The endocranial dural carpet is so firm over the whole of the dorsum, whatever its type, that anything in the nature of mechanical pull would seem to be thereby invalidated. (*e*) Finally the early chondrification of the interclinoid (*vide infra*) is certainly not devoid of significance,

and would appear to invest this element with a definite morphological value of its own quite apart from local mechanical considerations.

Some years ago Professor Fawcett drew attention in this *Journal* (vol. XLIV (3), 1910) to the separate chondrification of this uppermost part of the dorsum sellae in 19 and 21 mm. human embryos of his own and Professor Minot's collecting, and remarked further that Fischer had met with an identical condition in the monkey. These findings elicited a special Anatomical Note in that issue of the *Journal* and have since been incorporated into certain of the standard text-books of anatomy, without, however, any suggestion as to causation of the phenomenon. Fawcett's figure, a sagittal section through the skull base and upper cervical region of a 19 mm. embryo, shows the future interclinoid element, already chondrified, situated at the rostral end of the parachordal plate, loosely connected thereto, and directly posterior to the pituitary; it shows also what may be considered a suggestive feature—the post-chordal bow of the atlas vertebra lying just cranialwards of the atlas centrum (dens).

Bearing in mind these topographical relations, and recalling that the parachordal region of the basis cranii is the morphological equivalent of vertebral centra, it is perhaps not preposterous to suggest that the interclinoid element represents the most cranial member of the whole series of post-chordal bows, here retained for functional convenience. For just here, where the notochord ends, tissue is available for structural requirements which elsewhere in the vertebral system would become a post-chordal bow. The bow is certainly retained in the first cervical segment as the ligamentum transversum atlantis in obedience to functional demands, and this retention is a hint as to the probable sequence of events in the more compressed and complicated parachordal region. In the absence of a satisfactory mechanical explanation of the individuality of the interclinoid portion of the dorsum the tentative suggestion is made that this part of the sphenoidal complex is in the nature of a post-chordal bow.

Professor HILL said that he had seen the bar described by Dr Cave in the Monotreme Skull.

Professor HARRIS alluded to the calcification of the pituitary body, in "pituitary dwarfs."

Dr J. KIRK read a paper by Dr A. H. BAKER and himself on "Congenital atresia of the small intestine associated with an unusual development of the pancreas and spleen." This will be submitted for publication in the *Journal of Anatomy*.

Dr ODGERS, Professor HARRIS, Professor WALMSLEY and the PRESIDENT discussed the paper with special reference to the parts played by the entoderm and mesoderm in producing the atresia, the nature of the portion of the pancreas which was present in the specimen, and the absence of the splenic artery.

Professor LE GROS CLARK read a paper on the "Medial geniculate body and nucleus isthmi," which will be submitted for publication in the *Journal of Anatomy*.

Dr U. V. NAYAK made the following communications:

(1) Note on an unusual type of cervical rib in a lemur.

(2) The wrist-joint and carpus in *Chiromys madagascarensis*.

Professor H. A. Harris with Audrey E. Russell made a communication, on the "Fundamental factors in the nutrition of cartilage and bone."

By using the method of fixation employed by Evans and Swezy in their studies on human chromosomes it has been possible to display active mitosis in the cartilage of human embryos. The zone of mitotic activity at the end of the long bone is continuous over a surface which can be divided into two portions, one of which, curved in conformity with the end of the bone, lies some distance below the hyaline cartilage of the joint surface, the other lies on the epiphysial side of the growth cartilage. This predetermination in cartilage and calcified cartilage occurs before mechanical factors such as muscle pull can be brought forward as sole determining factors.

The distribution of mucoid degeneration in cartilage is found to follow the localization of the mitotic annulus in a series of cases extending from achondroplasia to conditions such as "stippled epiphyses" and congenital dislocations of the long bones. Irregularities in the vertebral column of achondroplastic foetuses and children presenting stippled epiphyses with congenital cataract were illustrated radiographically and histologically. In all such cases the perversion of growth is due in the first place to mucoid degeneration of cartilage.

Professor Johnston expressed a doubt whether there was a complete death of the central cells, and asked what was the cause, if not due to defective nutrition from insufficient blood supply.

Dr Cave enquired what was the true function of an epiphysis. The growth of the bones in Reptiles takes place without them.

Professor Blair raised the question whether there was a maximum limit to the amount of glycogen which was used in the metabolism of cells, and whether the death of cells might be due to a surfeit of glycogen.

The President referred to the defective development of the ends of the bones in congenital dislocations, e.g. of the heads of the femurs in congenital dislocations of the hip joint, and asked what was the cause of this derangement of ossification. Was it due to an intra-uterine disturbance of the normal calcium metabolism arising from some change in the blood? He also alluded to the formation of Heberden's nodes in rheumatoid arthritis.

Professor Harris in reply to Dr Cave's question said that in birds the annular arrangement of mitotic figures is flattened out, and, that provided the epiphysis is flat, calcification in it does not take place. Presumably a similar condition was present in reptiles.

Professor J. L. Shellshear read a paper on the "Arterial supply of the cerebral cortex in Man," and with Dr A. A. Abbie a paper on the "Arterial supply of the cerebral cortex in the gorilla." These will be submitted for publication in the *Journal of Anatomy*.

Professor Le Gros Clark congratulated the authors on the strong evidence which they had demonstrated with regard to the constancy of the blood supply of the striate area by the calcarine artery. He also stated that the granular area of the frontal cortex was not an extension forward of the motor cortex but that it belonged to the insular area.

Dr Yoffey said that one was perhaps too easily inclined to believe that the rest of the brain follows the same rule as that of the calcarine artery and the area striata. It was difficult to assign a functional importance to every area, e.g. the temporal region supplied by the middle cerebral artery.

Dr KIRK alluded to the upper and lower parts of the Sylvian Fissure which corresponded to the areas of heard and of spoken speech supplied by the same artery, the middle cerebral.

The PRESIDENT enquired whether any functional differences had been noted in cases of asymmetrical arrangement of blood vessels, e.g. in the circle of Willis, the internal carotid or vertebral arteries. He also asked whether there was any division between the arterial supply of the upper limb area of the precentral gyrus and the lower limb area.

Dr G. S. SANSOM gave a demonstration on the "Early stages in the development of *Crocidura*."

Lantern slides were shown to demonstrate the cleavage process and formation of the blastocyst in the musk shrew (*Crocidura coerulea*).

One point of interest is the presence in the early blastocyst of a reticular endoderm surrounding the almost centrally situated mass of embryonal ectoderm. This recalls the condition of the extra-embryonal endoderm described by Gérard in *Galago*.

Professor HILL congratulated Dr Sansom on the excellence of the beautiful series of specimens which he had prepared and alluded to the important bearing that they had on the question of the nature of the reticular tissue which is present in the early blastocyst.

Professor J. P. HILL demonstrated a cinematograph film illustrating the "Early development of the rabbit ovum," which had been prepared by Warren H. Lewis and P. W. Gregory.

JUNE, 1933

The Summer Meeting of the Society was held at the University of Birmingham, on 23 and 24 June 1933. The President, Professor WRIGHT, in the Chair.

Dr R. H. HUNTER read a paper on "The ileum at the ileo-caecal junction." In discussing the ileo-caecal region it has become customary to quote a book published in 1914 by Rutherford, in which it is stated that there are no ileo-caecal valves. A later publication by the same author, made in 1926, is completely ignored, and in it Rutherford withdraws this statement, and shows by microscopic evidence that not only do valves exist at this point, but that they contain muscular tissue. Rutherford makes the comment that this muscle tissue probably represents the caeco-colic sphincter of lower forms, but he does not bring forward any evidence in support of this view. The presence of a caeco-colic sphincter has been questioned, but microscopic sections of the caeco-colic junction clearly demonstrate its presence, and its changing relation to the opening of the ileum. In the mongoose it forms a thickening of the inner muscle layer at a considerable distance above the level of the ileo-caecal junction. In this animal there is no ileo-caecal valve. The marmoset shows the same thickening of the caeco-colic sphincter, but close to the ileo-caecal junction. In the higher primates and in man the caeco-colic sphincter becomes incorporated in, and forms the muscular framework of, the ileo-caecal valves. A series of macroscopic and microscopic photographs of various mammals were shown to demonstrate these changing conditions.

In a series of human caeca the terminal 6 in. of the ileum were ligatured off, and also the proximal 6 in. of the colon. Into these caeca liquid gelatine was injected, and it was found that in some of them the gelatine found its way into the ileum, and in others it was confined to the caecum and colon. Further examination of the specimens showed that those with gelatine in the ileum presented a constant relation of caecum to ileum. The ileum presented a "horse-neck" bend and opened into the caecum at approximately right angles to the median wall of the caecum. At death the ileo-caecal sphincter is relaxed, and the gelatine was free to pass into the ileum in this position. In those specimens in which the gelatine had not entered the ileum, the latter lay against the caecal wall, and was flattened against it. The lower flap of the valve here prevented the gelatine passing from caecum to ileum.

Evidence in support of these views was found in X-ray photographs of living subjects, and in patients in whom the terminal ileum had been found at operation to be held fixed, by peritoneal bands, in an ascending position, and unable to form the "horse-neck" bend.

Professor T. B. JOHNSTON enquired whether a caeco-colic sphincter was constantly present in mammals. Professor Hunter replied: That consistently throughout the mammals examined microscopically there is always a definite caeco-colic sphincter.

The PRESIDENT alluded to a case reported by Mr Rendle Short who had observed the intermittent passage of fluid material from the ileum to the caecum. Professor Hunter replied: We must not allow ourselves to lay too great value on the study of this region under such abnormal conditions as those observed by Mr Rendle Short. Small amounts of material can be seen passing at short intervals from ileum to caecum, "like puffs of smoke" under the fluorescent screen. These, however, do not occur at the rapid rate suggested by Mr Short.

Dr P. N. B. ODGERS demonstrated a case of "Non-rotation of the gut in a woman of 87." This woman had been an inmate of a mental hospital since the age of 19 and had never had any illness; she died of senility and influenza.

When the abdomen was first opened, the large intestine was found to occupy the whole of the left half of the cavity, while the caecum lay just on the brim of the true pelvis to the left of the mid-line up against the descending colon, with the ileum entering its right side and the appendix springing from its anterior surface. On turning up the intestines there was no normal attachment of the mesentery of the small intestine: this was only represented by a few slight adhesions to the posterior abdominal wall along the upper portion of the superior mesenteric vessels. The jejunum, ileum, caecum, ascending colon and the right half of the transverse colon shared a common mesentery, which was attached along the anterior border of the pancreas and which was continuous on the right with a short, but well-marked mesoduodenum and on the left with a normal transverse mesocolon. The peritoneal relations of the remainder of the large intestine were normal: the descending colon had been normally laid back against the posterior abdominal wall. The duodeno-jejunal flexure was to the right of the mid-line and to the right of the superior mesenteric vessels. After their removal, the jejunum and ileum were measured and were only 8 ft. 8 in. in length. While very different measurements have been given in formalin-fixed bodies, 12–13 ft. appears to be an average length and

certainly this portion of the gut must have been abnormally short in this woman. The head of the pancreas was very much less developed than usual: there was no uncinate process.

The duodenum. The first and second parts of this were normal in position, but the third portion, instead of running transversely, was directed dorsalwards behind the second part to end in the duodeno-jejunal junction, which was similarly situated. There were two sharp kinks, one at the junction of the second and third parts and another at the duodeno-jejunal flexure. There was no muscle of Treitz, some indefinite subperitoneal condensation running up from the flexure being quickly lost over the superior mesenteric vessels. There was, however, a well marked peritoneal fold connecting the right side of the duodeno-jejunal junction with the parietes, and this was apparently its only means of fixation. In all the recorded cases of non-rotation of the gut, where any mention is made of the position of the duodenum, the duodeno-jejunal flexure is constantly stated to be situated to the right of the mid-line, but there is only one other case, in which the duodenal curve was exactly similar to this one, and that was also associated with a non-rotation (Telfer, *J. Anat.* 1914–15, vol. XLIX, p. 136).

This failure of the duodeno-jejunal flexure to cross the middle line must be due to some lack of development of the retention bands, one fixing the colic angle and the other the flexure, which are both obvious at the 35 mm. stage and which normally keep these two points approximated. The correct apposition of these latter must be a primary factor in producing the subsequent normal disposition of the intestine returning from the umbilical sac.

Dr J. B. BAXTER read a paper on the "Development of the vagina in the pig," which will be submitted for publication in the *Journal of Anatomy.*

Professor BEATTIE alluded to the views of Wood Jones on the development of the vagina in *Dasyurus*, and said that an investigation of other Marsupial forms was desirable.

The PRESIDENT suggested that great variations in the condition of the vagina should be correlated with the variable conditions met with in the Metatheria and that a study of the development of the vagina in Marsupials was well worth while. He also recommended the study of the genital organs in the pig which is a most primitive animal, as are also the Insectivora.

Mr M. A. MACCONAILL (in association with Mr F. L. RALPHS, M.Sc.) read a paper on the "Regulation of post-natal growth in simple organs," which will be submitted for publication in the *Journal.*

Dr YOFFEY observed that while not disputing the general validity of the laws of growth propounded by Mr MacConaill, he felt that they could not apply to most tissue cultures, where growth very definitely was *not* uniform in all directions.

In reply Mr MACCONAILL said that no great stress was put on the postulated uniform growth of cell cultures *in vitro*. The main point was the demonstration of a mechanism of regulation which permitted adaptation of the growth of one organ to that of associated parts and yet preserved the predetermined adult form. Form was not a static end-result, but was the exhibition of a dynamic mechanism capable of exact quantitative expression.

Dr YOFFEY read a paper on "The age of thoracic duct lymphocytes." He commenced by observing that the data communicated to the Society in his previous communication had now been fully confirmed, by twenty-three additional experiments. The fundamental fact that in the normal dog the blood lymphocytes were replaced between two and three times daily could now be regarded as established on a firm experimental basis.

In recent years Wiseman, working under Sabin, had attempted to show that the lymphocytes in the blood were largely old and mature cells. As far as the lymphocytes which entered the blood via the thoracic duct were concerned, he wished to submit evidence to prove that they were young and active cells. (1) They were cells which had just been formed in the glandula mesenterica magna. Specimens of the glandula mesenterica magna were submitted to illustrate the size of this organ. (2) Tissue culture experiments had shown that the lymphocytes of thoracic duct lymph—and for that matter those of the blood also—possessed great developmental potentialities. (3) The thoracic duct lymphocytes contained abundant mitochondria. (4) Adopting Wiseman's own favourite criterion of youth, the cells were markedly basophilic when stained with Wright's stain.

Professor BEATTIE discussed various theories on the origin and fate of the blood lymphocytes and in particular the commonly accepted view which postulates that cells are mobilised from the endothelium, transported to different parts of the body and are eventually destroyed in the bone-marrow.

Dr YOFFEY replied that it was difficult at the present time to make any positive statements with regard to the various theories on the origin and fate of the lymphocytes. The whole question of the reticulo-endothelium was in a chaotic condition. He himself believed that lymphocytes were produced in the glandula mesenterica magna and that they were transported from thence via the thoracic duct into the general blood stream.

Dr THOMAS NICOL made two communications. (1) "Variations in the oestrous cycle in the virgin guinea-pig, after parturition, and during pregnancy." This communication embodied the results of work on the oestrous cycle in *Cavia* undertaken in connection with researches on intravitam staining with trypan blue. Daily vaginal smears were taken from 40 animals over about nine months, and 368 cycles were recorded and analysed statistically. It was confirmed that the normal cycle in *Cavia* was 16–18 days with a normal variation in a series of consecutive cycles of one to two days. Variations from the mode might be considerable, cycles from 10 to 26 days having been recorded, and furthermore a cycle was in some cases apparently missed. Some animals had a totally irregular rhythm and this irregularity in individuals was proved to be statistically significant. No seasonal variation occurred in the stock of animals kept at a uniform temperature. In young animals at the onset of puberty the first two or three cycles were often prolonged and irregular, generally speaking, and thereafter a regular rhythm was abruptly established and maintained. Practically similar observations were recorded after parturition in mature animals allowed to suckle their young. Some animals showed apparently definite vaginal oestrous signs during pregnancy.

(2) "Post-partum repair of the uterus of the guinea-pig and the associated appearances in the ovaries." This paper analysed certain cases observed in which there was variation in the rapidity of repair of the endometrium after

parturition. It was shown that repair in a normal animal not re-impregnated was completed in 4½–6½ days after parturition; if impregnation had taken place repair was accelerated, the acceleration not being due apparently to ovarian conditions, but probably to the presence of the fertilised ovum itself in the tube. In animals in which normal ovulation had not taken place, post-partum repair was found to be greatly delayed. The examination of the associated ovaries led to the conclusion that the proximate cause of the delay was due to the absence of young corpora lutea, the possibility of failure of action of the pituitary hormones being also kept in view.

Dr W. J. HAMILTON gave a lantern demonstration of "Living mammalian ova." The ova dealt with were mainly those of the ferret, with a few examples of guinea-pig. The specimens from the ferret formed a continuous series from the unsegmented fertilised ovum to the stage of the free blastocyst of nine days showing differentiation of the inner cell mass. In the earlier stages the extensive size of the perivitelline space was demonstrated. In this space the egg is free to move and the polar bodies are not located in any precise position relative to the circumference of the ovum. He pointed out the importance of controlling investigations of fixed material by observations on living specimens and showed the result of fixation on ova and blastocysts.

Professor HUNTER alluded to the difference in opinion on the question whether inequality in size of the first two blastomeres of the mammalian ovum was to be regarded as abnormal or normal.

Dr HAMILTON replied that if the material was grouped statistically the variation is not significant.

Professor R. D. LOCKHART presented a communication illustrating "Muscles in action—surface anatomy by cinema."

A film was shown illustrating the use of the cinema in teaching the action of muscles and their influence upon the surface contour of the body. Different types of muscular development were shown by contrasting the model, specialising in muscular development, and a team of professional acrobats executing various somersaults in ordinary and slow motion.

The clinician's method of reinforcing the action of muscles was used, and the action of such a muscle as the deltoid in raising and also lowering the arm was graphically demonstrated by allowing a heavy weight to ride upon the muscle during the movement of the arm, and observing how it suddenly sinks into the arm when resistance is opposed to lowering.

The reels shown were part of a film recorded for Professor R. D. Lockhart by Messrs Kodak, Ltd., and published in their Medical Film Library, with the title:

"The Action of Muscles, Vertebral Column, Hip and Shoulder Joints, in Living Subjects." No. 236. The living anatomical model, Part I, 2 reels. No. 237. Male acrobats, Part II, 1 reel. No. 238. Female acrobats, Part III, 2 reels.

Mr H. M. ROUND gave a communication and cinema demonstration on the "Action of the palate and superior constrictors."

Dr J. A. LANCHESTER read papers on (1) the "Permanence of visual impression" and (2) "A vertical hiatus in the retina."

Professor WOOLLARD referring to the "blind spot" said that he was inclined

to agree that compensation for the blind spot would most often be central in the same way as, in hemianopia, an image falling partly on the normal and partly on the blind part of the retina is reconstituted centrally. With reference to the "Hiatus of the retina" he said that he was previously unaware of this defect, but its situation strongly suggests that it lies between the nasal and temporal halves of the retina. Some years ago, he had made serial sections of the retina in a large number of Primates and in Man. In these he had not encountered any histological basis for this hiatus in the retina itself.

Professor R. D. LOCKHART said: "Dr Lanchester bears a name famous in engineering and aeronautics. In this Department we have found his incursion into the domain of medicine stimulating and provocative. In addition to seeing his experiments confirmed upon students and members of the Staff of this department, the opportunity was taken of submitting his conclusions on the existence of a vertical hiatus in the retina to Professor Brouwer of Amsterdam, who replied that he and his colleague, Professor W. P. C. Zeeman, the Ophthalmologist, readily confirmed Dr Lanchester's experiments, though they were not prepared to accept his explanation."

Professor S. E. WHITNALL with Professor J. BEATTIE contributed a communication on "Exophthalmos: an anatomical criticism of the theories of its causation; together with the results of experiments on the cat." Most theories of its causation (particularly in connection with hyperplastic toxic goitre) are based upon the supposition either of over-stimulation of the involuntary musculature in the orbit, or of increase in the retro-ocular contents. The involuntary musculature concerned may be considered in three regions: palpebral, periorbital, and vascular.

(i) The palpebral musculature (Müller's m.m. palpebrales sup. et inf.) can explain the eyelid signs of Dalrymple, Stellwag, and Graefe. The scattered fibres in the cheek-ligaments of the lateral and medial recti muscles serve merely to draw back the conjunctival fornices in movements of the eyeball. The "capsulo-palpebralis" fibres comprised by these two groups are placed too far forward to substantiate Landström's theory of a cuff-like ring being able to squeeze the globe forwards.

(ii) The periorbital musculature (Müller's m. orbitalis) in lower animals forms a broad well-defined sheet filling in the wide gap in the bony lateral orbital wall, and is easily displayed in the dog, sheep and cat. Here stimulation of the cervical sympathetic in the neck has been shown by several experimentalists to cause definite protrusion of the eyeball by contraction of the orbitalis muscle when the head vessels were tied, and also when the head had been severed and completely drained of blood (Macallum and Cornell). But in man this muscle is represented by a mere vestige only, tucked away deeply in the inferior orbital fissure, and incorporated to such extent with the periorbita that it could not possibly act as a protrusor by pressure on the mobile orbital contents. Nor does it appear likely that this muscle can cause engorgement of the retro-ocular venous system by compressing either the few venules which may possibly traverse it or the main ophthalmic veins as they leave the orbit at its apex to enter the cavernous sinus.

(iii) An explanation of the sign was sought in the condition of the perivascular musculature in the walls of the venules, the bulk of which lie behind the eyeball. Experiments were conducted by means of stimulation of the

cervical sympathetic, obstruction of vessels, and the action of drugs on cats. Contraction of the palpebral muscle, as a check, and protrusion of the eyball were so contrived as to be registered simultaneously on the drum.

(*a*) Stimulation. There was a marked difference between the two in response to stimulation of the cervical sympathetic in the neck. The eyelid contracted at once, remained steady during the excitation, and quickly returned to normal when this ceased. Whereas the eyeball protruded immediately (probably the orbitalis effect), but showed a much slower return to normal position afterwards, and then, by a slight enophthalmos or recession, even indicated a "rebound" (suggestive of a secondary and vascular effect). Repeated stimulation at the end of each cycle showed unvarying contraction of the eyelid as before, but a slight progressive degree of enophthalmos or rebound of the eyeball.

(*b*) Obstruction or occlusion of vessels: there was definite protrusion of the eyeball on stimulation of the cervical sympathetic with the carotid arteries clamped (presumably due to contraction of the orbitalis), but this was repeatedly followed by increased protrusion when the vessels were released (suggestive again of a secondary and vascular action). Again, without excitation of the sympathetic, clamping the external jugular veins caused slow protrusion of the eyeball continuing until released, as has been observed by others. Clamping the carotid arteries caused a marked enophthalmos with return to normal position when released. The last two experiments suggest an over filling of the retro-ocular venous bed when the veins are clamped and a lack of fullness in the bed when the arteries are clamped.

(*c*) Drugs: several are known to cause exophthalmos. Injection of paraphenyl-diamin was shown by Troell to drench the orbit specifically with exudate, and acetyl-choline, which causes dilatation of the vessels by paralysis of the nerve-endings in their walls. Both drugs cause protrusion of the eyeball with the cervical sympathetic (and therefore the orbitalis muscle) put out of action.

In our experiments on cats, injection of acetyl-choline gave a transient enophthalmos or recession of the eyeball, possibly due to the rapid fall in blood pressure, which this drug causes, reacting on the retro-ocular venous bed. This was at once followed by protrusion of the eyeball on the return rise in blood pressure, with a slight rebound as before.

Finally, acetyl-choline was injected into a cat whose cervical sympathetic ganglion had been removed two months previously (the orbitalis muscle being subsequently found degenerated). Exactly similar results to the last experiment were observed.

It therefore seems permissible to conclude that exophthalmos in the cat can be caused by two separate factors. Firstly by the action of the orbitalis muscle alone, as supported by Macallum and Cornell's result of stimulating the cervical sympathetic with the head drained of blood; and secondly by the action of a drug on the retro-ocular venous bed, as supported by our last experiment where the orbitalis was out of action.

Professor WOOLLARD remarked that in man unstriped muscle was regarded as incompetent to produce proptosis. The veins anastomosed so freely that venous engorgement was unlikely to be the cause and that stimulation of the sympathetic did not cause nor did section of the sympathetic relieve exophthalmos.

Dr Tudor Jones described "The subdiaphragmatic connections of the phrenic nerve," in a human adult, three newly-born infants and several guinea-pigs with particular reference to the connection between this nerve and the sino-auricular node discovered in an embryo of 24 mm. The general arrangement of the nerve on the right side accorded with the description of Luschka and the drawings of Hirschfeld. The nerve divided into two principal divisions immediately above its entry into the central tendon of the diaphragm. Of these, the posterior soon became the larger by increase in the number of its myelinate fibres and the addition of large bundles of amyelinate fibres. Buried in the muscular part of the diaphragm, it still further increased in size, but was here subdivided into a symmetrical pattern of five large nerves, of which the middle three were threaded together from above downwards by a myelinate band. The larger part of these three nerves was either amyelinate or ganglionated or both. The ganglionated parts were gathered together into a single elongated ganglion, which, together with a large single bundle representing the post-ganglionic fibres of the ganglion, disappeared behind the inferior vena cava. An ascending and a descending branch of large size, entirely amyelinate, represented the termination of this nerve on the inferior vena cava. Below the ganglionic portion, which was buried in the diaphragm, the main extension of the phrenic nerve was continuous with the phrenic ganglion by means of an amyelinate bundle, and the phrenic ganglion in its turn communicated with the semi-lunar ganglion, the solar plexus, the suprarenal plexus, the aortic sympathetic plexus and (possibly directly) with the vagus. The system as a whole seemed to be concentrated upon the inferior vena cava and the hepatic veins—in other words, in consideration of findings which at present were demonstrated for rodents only (apart from the human embryo)—upon the derivatives of the sinus venosus. The diaphragmatic branches themselves were much smaller than the chief vena caval branches, and were mixed.

Bielschowsky preparations had been made of the semilunar ganglion and its connections, the phrenic ganglion and its connections, and a portion of the solar plexus. The great and small splanchnic nerves and the vena caval branches of the phrenic nerve had been sectioned and stained by Mallory's method; and the phrenic nerve itself throughout its extent had been excised, portions at different levels being prepared for staining by Weigert's method. In this way it was shown that the amyelinate fibres of the lower part of the thoracic phrenic nerve and all its branches in and below the diaphragm had their origin in the newly described intra-diaphragmatic ganglion, and entered the main trunk of the nerve in that part of its course which lay between the ganglion and the upper limit of the muscular part of the diaphragm. The phrenic nerve in relation to the superior vena cava contained no bundles of amyelinate fibres, although a few scattered fibres might be contained within it. The constitution of the symmetrically divided part of the system showed that most, if not all of the preganglionic fibres (i.e. myelinate fibres), were distributed through the phrenic nerve.

Whole preparations of the thoracic and subdiaphragmatic viscera of guinea-pigs stained by the vital methylene blue method gave a view of the conditions in the neighbourhood of the inferior vena cava not at present attainable in man. Such preparations showed that a dense plexus of nerves surrounded the inferior vena cava at its entry into the thorax. The constituent nerves came from the phrenic nerve and from all other available sources. The inferior

vena cava in the guinea-pig was relatively much longer than in man, and it was of interest to observe that the bundle of nerves contributed by the phrenic nerve to the inferior vena caval plexus reached it mid-way between the diaphragm and the heart. This fact was to be considered with reference to the development of the sinus venosus, and the elongation of the inferior vena cava in the guinea-pig. The phrenic contribution could be traced headwards among the constituent branches of the plexus to the situation of the sino-auricular node. It could be said, therefore, that the system in the adult guinea-pig had the same distribution as in the human embryo, and that only the small part between the inferior caval plexus and the sino-auricular node remained undemonstrated in the human adult. A communication from the phrenic nerve on the left side could be traced to the left suprarenal plexus and semilunar ganglion. Its small size accorded with the absence of a left inferior vena cava.

Mr MacConaill enquired whether Dr Jones had investigated the relation between the ganglia described and the so-called "mediastinal ganglia" lately found in man?

Dr Davies enquired if the fibres in the branch which Dr Jones described going from the right phrenic nerve to the sino-auricular node contained medullated or non-medullated fibres? Dr Jones replied that they were non-medullated. Dr Davies then suggested that, as the branch seemed to be inconstant, the non-medullated fibres might represent an aberrant path of sympathetic fibres from the inferior cervical ganglia *via* the phrenic nerve to the heart.

In reply, Dr Tudor Jones said the ultimate fibres passing from the plexus of nerves on the inferior vena cava of the guinea-pig to the situation of the sino-auricular node were amyelinate. Concerning the derivation of the ganglia and their post-ganglionic fibres in man, it could be stated that the ganglia described, the new ganglion, the phrenic ganglion, and the semilunar ganglion, were similar in appearance. All contained some bipolar cells, "Kronenzellen" and star-shaped cells of medium size. Attention should be drawn again to the fact that the total distribution was identical with that in the embryo of 24 mm. The developmental changes in the relative positions of the diaphragm and the sinus end of the heart accounted for the elongation of the phrenic connections with the derivatives of the sinus venosus. It should be remembered that in the embryo nerve cells were absent from this nervous formation throughout its extent. A much better understanding of the minute anatomy of these synaptic centres than we now possessed was necessary for the understanding of the very complex series of connections which had been described. Until more was known of these matters, mere assignment of fibres to either the sympathetic or the vagus was academic.

Professor Beattie (with Dr D. L. Thomson) read a paper on "Studies in living gland cells."

Dr Yoffey enquired whether the mitochondria had been investigated by the Janus Green stain; whether they occurred in any constant position in the cell; and whether they showed any sign of diminution in older cells. Furthermore, he enquired whether they became less after the cells had been stimulated by acetyl choline.

Dr Pickworth gave a paper on "New method of investigating the brain capillaries and its application to the study of the brain in cases of mental

disease" illustrated by lantern slides and stained sections also shown as lantern slides. In the discussion which followed:

Professor SHELLSHEAR after congratulating the author, said he had been looking for such a method for many years. He noted from the illustrations that each layer of the cortex had its characteristic pattern of capillary blood supply, and suggested that further investigation of this would be very useful.

Professor WOOLLARD also congratulated the author but said he would not go as far in saying that the method would demonstrate histologically the region of the brain concerned with the mind, but he was very interested in the pathological condition of the capillaries shown. He asked if there was any relation of the stain used to the demonstration of iron by the Spatz method.

Dr TUDOR JONES asked what was the effect of the stain upon empty vessels.

Professor BLAIR pointed out the clear demarcation, in some of Dr Pickworth's beautiful preparations, of two layers in the cerebral cortex; a deeper layer with a very rich capillary network and a superficial one less richly supplied. This recalled the differential staining of similar cortical zones in the Spatz reaction which Dr Davies and he himself had shown probably depended in part on physical factors (*J. Anat.* vol. LXVI). A richer capillary pattern in the deeper layers of the cortex would certainly help to explain the deeper staining of that layer in the Spatz reaction.

Dr PICKWORTH in reply said that the method depended upon the presence of normal haemoglobin, and therefore empty vessels would not show any stain. In conditions of anaemia however the vessels were rarely entirely empty and showed as a somewhat broken appearance of fine lines and dots, the vessels were however readily distinguished. This condition was shown by anaemic animal brain as obtained by decapitation and contrasted markedly with the areas of vascular deficiency in the brains from Mental Hospital patients where no trace of almost empty vessels was to be found. All grades were seen between this through the stage of degenerated eosinophil tissue to entire absence of tissue. The vascular change shown by the new method was undoubtedly the earliest change possible that could be demonstrated histologically. He thanked the speakers for their remarks and their suggestions for future application of the method.

Dr HUGH DONOVAN read a paper, with which Professor OSMAN HILL was associated, on "The fascial relations of the tensor fasciae latae." The tensor bed is formed of fascia of varying texture, some of which is merely a condensation of areolar tissue between muscles. In the lower part of the bed, in relation to the vastus lateralis, and in the upper part in the cleft between the rectus and the glutei, the bed is dense and ligamentous in character. Elsewhere, i.e. over the glutei and the rectus, the bed is translucent and not worthy of special notice.

With regard to the thick almost tendinous band; traced upwards it narrows to be attached to the hip bone in the region of the straight head of the rectus, both above and below this tendon; it is attached to the tendon itself, to the hip bone below the tendon, and to the capsule of the hip joint. Where the band passes under the straight head of the rectus to the joint capsule it ceases to be part of the tensor bed, and below the point of attachment to the capsule of the joint it is in the same plane as the areolar tissue septum between the

rectus and vastus, but such a distinct change in the character of the tissue occurs as to warrant it being called a free edge, cf. semilunar fold of Douglas. Posteriorly this band-like part of the tensor bed appears to have a free edge along the anterior border of the fused glutei. Actually it is attached here to the great trochanter by a moderately strong leaf of fascia at right angles to its deep surface. Another fascial slip passes from the band's deep surface to the hip bone, deep to the reflected head of the rectus muscle.

It was suggested that the tendinous portion of the bed is worthy of some such special name as ilio-capsulo-aponeurotic band; that its strength argued a function such as to maintain the tension of the ilio-tibial band when the hip joint is flexed; that morphologically it represented the upper portion of the external intermuscular septum; and that an abscess from a tubercular hip in the common antero-lateral site pointed forwards below the anterior edge of this band.

Professor D. M. Blair with Dr F. Davies presented a communication on "The conducting system of the heart," which will be submitted for publication in the *Journal of Anatomy*.

Professor Woollard congratulated the authors on the excellence of the technique. He agreed that in different vertebrates and mammals the extension of ganglion cells beyond the auriculo-ventricular sulcus would vary. In the snake they are found near the apex of the ventricle, but in the cat for instance one did not find them beyond the sulcus. His general impression was that the nerve endings were invariably pericellular in position.

He thought the authors had contributed considerably to the knowledge of the relation of the sino-auricular node to the auricular muscle, and the course of conduction at the sino-auricular node and auriculo-ventricular node.

He further suggested that the subendocardial smooth muscle might be undifferentiated Purkinje and cardiac tissue since it was in protoplasmic continuity with recognizable cardiac cells.

Dr Tudor Jones seconded very warmly Professor Woollard's appreciation of the careful and important work of Professor Blair and Dr Davies. He thought that what he was about to say, might be interpreted as a divergence of opinion. It was not so much that he differed from Professor Blair and Dr Davies as that there was some misunderstanding which, for the sake of further advances, should be cleared up. Professor Blair said that no nerve fibres could be seen to pass into the conducting fibres, but appearances strongly suggestive of the conditions described in all other muscle were evident in the photographs shown. It was not a matter of interpretation so much as of detection. It was important that inferences should not be drawn from negative findings. Even proprioceptive muscle fibres had a motor innervation, and if the conducting musculature had no intra-protoplasmic—or rather hypolemmal—endings, the muscle was not only exceptional in this respect, it was unique. The first appearances of striation in the cardiac muscle of the human embryo as well as in the heart of Lepidosiren were in relation to the nerves, and they in their turn were in the situation of the described nodes and their extensions.

Professor Blair thanked the speakers for their appreciative remarks. To Professor Woollard's suggestion that the sub-endocardial smooth muscle might be undifferentiated Purkinje and cardiac tissue he could only reply that, so far, they had seen this smooth muscle best in adult hearts.

In reply to Dr Tudor Jones, Professor Blair said that Dr Davies and

himself had made a special search in their preparations for evidence of continuity between the ultimate branchings of the nerve ending and the cross striations of the muscle fibre, such as Dr Tudor Jones had previously described, but had failed to find this. Professor Blair pointed out in his paper the resemblance between the nerve-muscle association there described and the ordinary "sole-plate" motor ending of skeletal muscle; that this "association" was possibly hypolemmal was not denied, but no deeper extension of the nerve ending into the striate part of the Purkinje fibre had been observed.

Professor SHELLSHEAR gave a short summary of his communication on "The cortical representation of handwriting."

Dr J. F. BRAILSFORD communicated a paper on "Types of chondro-osteodystrophy."

Professor BLAIR enquired whether the cracks observed in the epiphyses were lamellar, or whether they were vascular channels? In normal bones vascular channels were found running into the epiphyses.

The PRESIDENT asked whether the dental condition of the patients had been considered?

Professor BRASH suggested the possibility that the striations which were observed, might have been produced by previous illnesses.

Dr BRAILSFORD in reply said that he was not prepared to say that the cracks which he had noted were not vascular in nature, but they did not appear to be such.

Dr A. J. E. CAVE made a communication on "The occipito-atlantal joints." Observations made upon a representative age-series of some fifty cervical spines, obtained fresh at autopsy, reveal that in both the occipito-atlantal and atlanto-axial articulations there occur quite definite and more or less circumferential retrosynovial fatty fringes such as the French anatomists describe for the latter joint although British textbooks usually ignore these structures in both joints.

In the occipito-atlantal joint this retrosynovial fat is augmented in quantity in two situations, (*a*) medially, above and behind the attachment of the ligamentum transversum atlantis, (*b*) antero-laterally, on a plane just anterior to that of the vertebrarterial foramen. In the former site a well-marked and constant fatty pad lies within the capsule in contact with a receptive non-articular area on the superior aspect of the atlantal lateral mass; its apex reaches to, or beyond, the point of constriction or subdivision of the upper atlantal facet, and the more this facet is divided the larger the fatty pad. It may be noted that in this region the capsule is thinnest and is sometimes perforated by the synovial membrane which passes out here to become continuous with the bursa between the odontoid neck and the transverse ligament.

The antero-lateral pad, not always evident, is smaller and is a mere local enlargement of the circumferential fringe. Occasionally a very similar enlargement occurs at the posterior part of the joint whilst more rarely the articulation manifests a distinct fringe or fold along the whole length of its medial aspect. In the atlanto-axial joint the retrosynovial fat is best marked antero-laterally and postero-medially where it overlies (in favourable cases) an appreciable area of the axial articular surface. Coronal sections through the occipito-atlanto-axial mass demonstrate these fatty fringes very clearly.

Dr C. P. MARTIN contributed a paper on "The comparison of the joints of the arm with those of the leg," which will be submitted for publication in the *Journal of Anatomy*.

Mr HENDRY read a paper on the "Extension of the knee joint: its production and maintenance." He produced evidence that the movement was entirely controlled by muscular action. He shewed photographs of a man who was able to bear his whole weight upon the flexed knee six weeks after sustaining a complete dislocation of the joint. Mr Hendry advanced the following conclusions:

(1) That movements of joints are due to muscular action only.

(2) That the shape of articular surfaces is the result of movement.

(3) That ligaments play no part in producing, controlling, or checking normal movements.

(4) That postural tonus in the lower extremity of man is in the flexors and adductors of the hip, in the ham strings and calf muscles.

Professor WOOLLARD commenting upon a case of dislocation of the knee with rupture of the crucial ligaments, asked if the patient, who had lost all confidence in his knee, would always have an unstable joint.

Professor LOCKHART congratulated Mr Hendry on his functional study of the knee joint and commented upon the undue importance ascribed to ligaments in controlling normal movements of the joint.

Dr KIRK was decidedly of opinion that the ligaments were actively concerned in the control of movements.

The PRESIDENT mentioned the abnormal antero-posterior movements obtained when the anterior cruciate ligament was ruptured, and described the operation Hey Groves performed for replacement of the ligament.

Mr NAUGHTON DUNN stated that he was coming to rely more and more upon Mr Hendry's opinion in knee joint conditions. He said that the operation devised by Alwyn Smith and Hey Groves had been almost entirely given up.

Dr MARTIN stated that whether locking was due to muscular action or not, he knew he could produce it in the cadaver when all muscles had been removed.

Dr YOFFEY pointed out that according to Mr Hendry's own slides Sherrington's views on postural and phasic contraction were not invalidated. It was quite easy to demonstrate upon oneself that if one stood with the knee joint firmly extended and palpated the patella, the patella was quite loose and could be easily moved. Under these circumstances it could not be muscle action which was maintaining the stability of the joint.

Mr HENDRY in his reply said that he had definitely referred to normal movements and these were produced by the individual himself. The movements referred to by Professor Wright and Dr Kirk were produced passively and were not normal movements. He did not deny that certain ligaments helped to stabilise a joint by tending to prevent abnormal movements, as for example lateral movement at the knee. If that were a normal movement, muscles would exist to produce it and others on the opposite aspect would be necessary to restore the mean position; each muscle group would be the means of checking the movement produced by the other. With reference to the case mentioned by Professor Woollard, if the patient had loss of confidence in the joint despite good muscles, then it would very probably be found that the menisci were damaged or displaced.

He was aware of Sherrington's work on postural tonus, but from the X-rays he had shown, it seemed to him proved that when quadriceps action became necessary to maintain the erect posture, a greater degree of contraction or tone was present than was the case in full extension.

Mr R. WALMSLEY read a paper on the "Development of the manubriosternal joint" which will be submitted for publication in the *Journal of Anatomy*.

The PRESIDENT congratulated Mr Walmsley on the excellence of his specimens and his demonstration and remarked on the contrast between the type of joint which Mr Walmsley had described in which there was only slight yielding movement and a diarthrodial joint.

Professor WEST enquired whether any other joints in the body were developed similarly by the secondary formation of a cleft in a continuous plate of cartilage.

Dr GLADSTONE in reply to Professor West said that in the human embryo about the 35 mm. stage the cartilages of the sternal ribs were directly continuous with the lateral borders of the sternum, and the joints were developed secondarily.

Dr J. D. BOYD read a paper on "The development and significance of the amphibian carotid body."

The appearance of the carotid body in the Amniotes at the time that the primitive branchial circulation changes into the post-branchial phase suggested that a study of its development in the Amphibia ought to be of interest in the attempt to give a phylogenetic explanation of the origin of the carotid sinus mechanism. The carotid body in the Tadpole appears during the early stages of metamorphosis as a thickening of the wall of an anastomosis between the afferent and the efferent vessels of the first functional gill arch. There is no contribution to the thickening by cells derived from the epithelial body of Maurer. This thickening increases in amount, encroaches on the lumen of the vessel and, later, by the development of lacunae within the thickening, a spongy organ is produced. The nerve of the third arch is very closely related to the developing carotid body and gives a small bundle of fibres which appear to end on the body. The histogenesis and mode of termination of this bundle of fibres have not yet been studied.

The physiological significance of the carotid body in the Amphibia is not certain. There appear to be three possibilities: (*a*) the established idea that the body is one of the mechanisms which subserve the function of separating the pulmonary and systemic venous bloods. There is no correlation between the presence of the carotid body in the different amphibia and the presence of the other mechanisms (e.g. interatrial septum and spiral valve) known definitely to be concerned with this separation. It appears, therefore, that this mechanical function cannot be the only function of the carotid body. (*b*) Endocrine gland. No phaeochrome cells were found in the body and there is no experimental evidence to suggest that it elaborates a hormone. (*c*) Neuroreceptor. There remains the very interesting possibility that the carotid body in the amphibia is analogous as well as homologous to the carotid body of the Amniotes and that in it are nerve-endings responding to pressor and chemical stimuli.

Dr DAVIES asked if special techniques had been used in looking for the chromaffin cells in the gland. Dr TUDOR JONES asked if the carotid body could be homologised with the organ of Pinkus.

In reply Dr BOYD stated that the usual bi-chromate technique had been used without finding any chromaffin cells, this had also been the experience of other workers. The organ of Pinkus had not been specifically considered but the whole question of a possible homology between the pseudobranch and the carotid body was under consideration.

Professor A. H. SIDDIQI read two papers, which are to be submitted for publication in the *Journal of Anatomy*, on: (1) "Abnormalities of the porta hepatis." (2) "Variations at the lower end of the femur in Indians."

THE CEREBRAL HEMISPHERES OF *LACERTA VIRIDIS*

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In a survey of the literature dealing with the anatomy of the reptilian fore-brain, one is struck not only by the wealth of descriptive detail, but also by the confusion in the terminology employed and the variety in the homologies which have been suggested. The descriptive detail is no doubt accurate so far as the technical methods in use allow. That the interpretations of this detail are so varied suggests that the methods themselves may be at fault, and have failed to reveal certain essential facts.

The method commonly used has been the microscopical examination of serial sections stained by toluidin blue for cells, or by the Weigert-Pal or a silver impregnation method for nerve fibres. In this work these same methods have been used on the brain of *Lacerta viridis*, and after each region of the hemisphere has been described, the findings are discussed in relation to those of other workers and in other reptiles. In this way a general view may be obtained of the facts which have been elicited by these or similar methods throughout the reptilian class. Such a general view will form the basis of a discussion of homologies in which the limitations inherent in the methods can be taken into account. It will help to show where disagreement between different workers has been due to gaps in our knowledge resulting from these limitations, and what lines of investigation should be followed in order to fill them. It will also be of value in suggesting a more uniform terminology, for there is no doubt that much of the confusion which exists in fore-brain morphology is due to the number of ill-defined terms which have been used in incompatible ways by different workers.

Certain difficulties peculiar to fore-brain morphology may be stressed at the outset. The structural analysis of the nervous system cannot be carried further than the neurone, so that morphological comparisons must ultimately be made between neurones and groups of neurones. Now the simpler methods of neurological histology which have been used here, and by most workers in this field, do not show two of the essential parts of a neurone, the cell body and the axon, in one and the same preparation. It follows that the relation between the two is often left in doubt, or, in other words, that whether an axon carries an impulse from another cell body to the one in question, or *vice versa*, cannot be clearly demonstrated. This is obviously a technical limitation of very great importance.

Secondly, in an investigation of this kind, the data must be almost all microscopical. The structures under consideration are groups of neurones which must be distinguished from adjacent groups, all of which have a very

similar histological structure. Boundaries are consequently often ill-defined, and sometimes invisible. This is not entirely the fault of the methods, but an inherent characteristic of a correlating mechanism like the fore-brain.

A third difficulty is implied in the principle of neurobiotaxis which has been elaborated by Kappers and his school. A group of neurones is liable to migrate from its original position under the influence of repeated stimulation. It follows that even where such a group can be delimited accurately, care must be exercised in comparing it with a similar group in another species, since position and relations may have been altered considerably by neurobiotactic migrations. The fibre connections will form a constant criterion for comparison in cases like these, but, as has been pointed out already, the methods in common use do not reveal them as clearly as could be desired.

It is clear then, that both the nature of the material and the technical methods employed provide a tempting field for the application of preconceived homologies, which are very difficult to prove or disprove. It is unfortunate that practically none of them can be checked by palaeontological investigation. In this paper the attempt will be made to discuss them critically, and, bearing in mind the technical limitations, to reaffirm those which are reasonably sure, to state clearly where doubt still exists, and possibly to indicate the lines along which this doubt may be removed.

The work has been done in the Anatomy Department of University College, London, under the direction of Prof. G. Elliot Smith. My thanks are due to him for advice and inspiration throughout its course. They are due too, to Dr Una Fielding and to Dr A. Durward for much helpful criticism and discussion, and to my technician, Mr C. E. Vangucci, for the staining and cutting of sections.

MATERIALS AND METHODS

The material available consisted of twelve brains of *Lacerta viridis*. They were all obtained immediately after death, and except when the technique required a different fixative, fixed at once in 10 per cent. formalin. Both Golgi and Cox-Golgi methods were tried, but each was a failure. Ranson's and Weigert's methods were also unsatisfactory, the latter as medullated fibres seem to be comparatively few in this brain. Bielschowsky's silver impregnation method was found to be the best for fibres, and the toluidin-blue method for cells. All brains were embedded in celloidin and paraffin before being cut. Complete series were made in each case, and those on which this work is actually based are as follows:

Series no.	Stain	Plane of section	Thickness
B 87	Toluidin blue	Transverse	12μ
B 97	,,	,,	12μ
B 99	,,	Sagittal	12μ
B 120	,, (Huber's technique)	,,	25μ
B 98	Toluidin blue	Horizontal	12μ
B 86	Bielschowsky	Transverse	12μ
B 102	,,	,,	12μ
B 109	,,	Sagittal	15μ

The most satisfactory series were B 87, B 99, B 102 and B 109, and most of the observations and figures were made from them. Figs. 2*a* and 2*b* indicate the approximate plane of section for series B 87 and B 102, from which figs. 3–10 and 12–16 were drawn respectively.

EXTERNAL FEATURES AND MAIN SUBDIVISIONS OF THE TELENCEPHALON

In its general features the telencephalon of *Lacerta viridis* does not differ greatly from that of most lacertilia and *Sphenodon*. It is of the macrosmatic type, with a well-developed olfactory bulb joined to the hemisphere by a peduncle of moderate length. Fig. 1, an outline drawing from a photograph, shows the main features. The accessory bulb forms a visible swelling behind the main bulb. In sections it can be seen on the dorso-medial aspect of the peduncle, where it receives the division of the olfactory nerve from the vomero-nasal organ. An accessory olfactory bulb has been described in a comparable position in many other Reptiles. It was not mentioned by Cairney in *Sphenodon*.

The term "olfactory peduncle" will be used only for the part of the olfactory apparatus which joins the bulb and accessory bulb to the anterior pole of the hemisphere. It is distinguishable from both regions by the absence of bulbar formation on the one hand, and of cortical formation on the other. Externally there is nothing to mark the junction between the peduncle and the hemisphere.

The general shape of the hemispheres can be seen from the drawing, fig. 1, and the sections, figs. 3–10. Laterally a fairly well-marked longitudinal depression forms the endorhinal fissure, Edinger's "fovea limbica externa." This fissure does not show well in the sections but can be seen in figs. 7 and 12. It lies along the ventral edge of the pyriform cortex and separates it anteriorly from a part of the corpus striatum, posteriorly from the amygdaloid. This posterior part of the fissure corresponds with the "amygdaloid fissure" of Johnston. Medially a slight depression can be seen along the ventral edge of the hippocampal cortex, as is shown in section in figs. 7–9. It begins anteriorly about the middle of the paraterminal body, and ends posteriorly at the level of the posterior pallial commissure. This fissure is very constantly present in Reptiles, and has been given many names. It is the "fimbrio-dentate sulcus" (Johnston, 1915), the "fissura arcuata" (Herrick, 1910), the "fissura hippocampi" (Hines, 1923), the "fissura septo-corticalis" (de Lange, 1911; Kappers, 1921) and so on. As Elliot Smith has pointed out (1903), it lies below the hippocampal cortex, and therefore cannot be homologous with the hippocampal fissure of Mammals. Johnston (1913) has suggested that the part of the brain in Reptiles which lies below the fissure in question really belongs to the hippocampal formation, but that it does not differentiate into definitive hippocampal cortex except in Mammals. He calls this region "primordium hippocampi" and homologises the fissure with the hippocampal fissure of Mammals. The evidence on

which these suggestions are based is not satisfactory, and the term first used in 1903 by Elliot Smith for this fissure in *Sphenodon*, the "fissura limitans hippocampi," is the most appropriate. It is unfortunate that even more confusion has been introduced by the application of the term "fissura limitans hippocampi" to a different and inconstant fissure in Reptiles (not represented in *Lacerta*) by Johnston and other American workers. This question will be discussed more fully later when the structure of the paraterminal body is described. There is no representative of the sulcus lobaris, the sulcus coronalis, and the sulcus longitudinalis, described by de Lange (1911). The fissura limitans medially, and the endorhinal fissure laterally, appear to be the only ones constant enough to be of comparative morphological value in the various orders of Reptiles.

For descriptive and comparative purposes it is necessary that the telencephalon should be divided into regions which can be treated separately. Any such division must, *ipso facto*, be artificial, and can only be justified in so far as it separates regions which have some anatomical, embryological, or functional claims to be considered apart from one another. Many such divisions have been suggested (e.g. by Elliot Smith, Johnston, Herrick, Kappers, etc.), which differ more or less according to the criteria which have been used in making them. Since the fore-brain was first differentiated for the reception and correlation of olfactory impulses, and since in the Reptile it is still dominated by olfactory impulses, the arrangement and connections of the olfactory apparatus might make a convenient basis for subdivision. This basis will be used here, but considerably modified for the sake of descriptive convenience. Its main lines were mapped out by Elliot Smith in 1901, and his terminology will be followed.

Anteriorly the individuality of the olfactory bulb and peduncle is obvious. Where the peduncle broadens to join the hemisphere it is surrounded by an undifferentiated layer of cells (fig. 3) which forms a secondary olfactory nucleus. This has been called by Edinger the "lobus olfactorius" and by Herrick (1924) the "nucleus olfactorius anterior." Herrick's term will be adopted here. These three structures, the bulb, the peduncle, the nucleus olfactorius anterior, can be grouped together as the first subdivision of the olfactory apparatus. From them impulses are transmitted to more highly differentiated regions of the hemisphere.

Laterally and ventrally are a series of structures which Johnston (1922) has suggested are concerned primarily with the correlation of olfactory and thalamic impulses. They include the corpus striatum, the amygdaloid nuclei, the pyriform cortex, and the nucleus of the lateral olfactory tract. The group is not very homogeneous since, although the pyriform cortex and amygdaloid nuclei are dominated by olfactory impulses, the striatum is dominated by thalamic and hypothalamic impulses, and in Reptiles has comparatively few olfactory connections. From a descriptive point of view, however, it is undoubtedly convenient to group these structures together, and there is some theoretical support for doing so, since there is evidence that, whatever may be its connec-

tions in Reptiles and higher Vertebrates, the oldest part of the striatum is primarily a centre for giving effect to olfactory impulses.

Ventrally, lying between the paraterminal body medially and the endorhinal fissure laterally, behind the anterior olfactory nucleus and in front of the amygdaloid nuclei, is an area called the tuberculum olfactorium (figs. 1, 4–7, 20). It is poorly differentiated in *Lacerta* and is closely related to the striatum and to the paraterminal body, but cannot easily be grouped with either. It will be described as a separate subdivision of the hemisphere.

Medially the wall of the hemisphere is occupied by a well-developed mass of tissue, which appears to serve chiefly as a relay station for impulses coming to or going from the hippocampal cortex. Many of these impulses are olfactory. This region has been given various names; here Elliot Smith's name, "paraterminal body," will be used.

There remains only the dorsal part of the hemisphere. This shows a well-differentiated medial part, the hippocampal cortex. Dorsally there is an area of cortex, clearly differentiated, the morphology of which is obscure. It has been called "parahippocampal" by Elliot Smith, "general cortex" by most American workers, and "cortex ammonis" by Kappers and his school. Here the non-committal term "dorsal cortex" will be used. Dorso-laterally the pyriform cortex can be seen. This has already been grouped with the structures in the ventro-lateral hemisphere wall following Johnston's suggestions (1922). This seems morphologically satisfactory, but for descriptive purposes it will be convenient to follow common usage by classifying it with the other two cortical areas.

Clearly this subdivision and grouping of parts of the hemisphere is a compromise, and receives its chief justification on the grounds of descriptive convenience. As was stated above, many attempts have been made to subdivide on morphological or functional grounds in such a way that the subdivision should be applicable throughout the vertebrate phylum. All of them, as one would expect, are open to criticism.

The various parts of the fore-brain are interdependent functionally. Although one part may be in a state of greater functional activity at any one time than another, the fore-brain works as a whole. This may no doubt be said of any part of the body, or indeed of the whole body, but it is particularly true of the fore-brain, which is essentially a correlating mechanism. It follows, since structure and function go hand in hand, that the attempt to make rigid morphological subdivisions in such an organ is likely to be of no avail.

A rough subdivision into "basal" and "pallial" regions has frequently been made, although accepted and implied more often than specifically stated and defined. Edinger (1908) made such a subdivision into "episphaerium" and "hyposphaerium," the former being pallial and the latter basal. It is a little difficult to see exactly what parts of the brain he means to be included in each of these subdivisions, but it appears that the hippocampal cortex, the pyriform cortex and the dorsal cortex are included in the pallial

part or episphaerium; the corpus striatum, amygdaloid, olfactory bulb and tracts, and paraterminal body in the basal part or hyposphaerium. It is obvious that structures which are very different functionally and morphologically are included in both these groups. Moreover, in the case of the pyriform cortex, there is some evidence at least that it is developed from the basal area (Johnston, 1916*b*), or that it is derived from Johnston's "lateral olfactory area" in Selachians (Johnston, 1922), and certainly its most obvious connection is with the lateral olfactory tract. On the medial side, the paraterminal body is very closely related to the hippocampus, so much so that Johnston, on embryological grounds, has been led to include part of it in the hippocampal formation as "primordium hippocampi" (Johnston, 1913). Whether one agrees with his view or not, it at least indicates the difficulty in making a rigid distinction between the two parts, a difficulty which was recognised by Elliot Smith (1903). Similar difficulties apply to the subdivisions which go even further, e.g. Herrick (1910), who divides the hemisphere into four quadrants, dorso-medial, dorso-lateral, etc. In this he has been followed by Kappers (1921). In the adult brain it is clearly impossible to fit the differentiated parts into these sectors without making obviously unnatural divisions, while in the embryo the names merely indicate certain topographical regions of the fore-brain vesicle which have not differentiated far enough to have clearly defined boundaries.

It remains true that, in a general way, the dorsal part of the hemisphere vesicle develops into a "pallial" area, a correlation centre of a high order, and that the ventral part develops into a large ganglionic mass under the influence of fibres which enter it from the cerebral peduncle, which may be called "basal." Both medially and laterally the two regions overlap in such a way as to make strict definition impossible.

The attempt at a subdivision on functional grounds has met with rather more success. Broadly, it is justifiable to distinguish: (i) a rhinencephalon, including the bulb, peduncle, anterior olfactory nucleus, pyriform cortex, amygdaloid nuclei, tuberculum olfactorium, paraterminal body, and hippocampal cortex; (ii) a corpus striatum connected predominantly with the thalamus and hypothalamus; (iii) the dorsal cortex. There is still doubt whether the dorsal cortex should be included in the rhinencephalon as parahippocampal cortex, or whether it should be looked on as the forerunner of the mammalian neopallium. Provisionally it is best kept separate. On the comparative morphological side this division has received considerable support and elaboration from Johnston (1922). Using his terminology, the rhinencephalon would consist of the medial, lateral, and basal olfactory areas of Selachians, together with the primordium hippocampi. To the corpus striatum he assigns a threefold origin: (i) a large part of what has been called the palaeostriatum (the "olfacto-striatum" of Cairney, Herrick, etc.) from the basal olfactory area, under the name of "bed of stria terminalis"; (ii) the remaining part (the so-called "somatic" striatum of Cairney, Herrick, etc.) from the area to which he

applies the name "somatic" in the telencephalon medium of Selachians, as globus pallidus and putamen; (iii) the greater part of the caudate nucleus as a new addition in the Reptiles from the lateral edge of the dorsal (his "general") cortex. This would leave an important overlap between the rhinencephalon and the striatum, since his stria terminalis bed is on these grounds primitively an olfactory centre. The amygdaloid nuclei he derives in part from the stria terminalis bed, and in part from an infolding of the superficial parts of the lateral olfactory area. It would therefore remain in the rhinencephalon. It is not quite clear whether the "primordium neopallii," which he distinguishes in Selachians, is looked upon already as a fundamental division of the fore-brain, or simply a differentiated part of the "somatic" area of the telencephalon medium. He obviously considers it to be homologous with the dorsal ("general") cortex of Reptiles. Enough can be seen from this very brief sketch of an elaborate and careful attempt to make consistent morphological subdivisions in the fore-brain to show that a great deal of overlap between the main functional division suggested above (e.g. between rhinencephalon and striatum, and between dorsal cortex and striatum), is inevitable, and becomes more marked as one ascends the scale from the fairly primitive Selachians.

It may be pointed out here that the term "somatic," as used by Johnston and many other comparative neurologists to contrast with "olfactory," will be avoided. There seems no reason why the olfactory sense should be any less "somatic" than, for instance, the visual or auditory senses. The essential difference between the olfactory and other sensory impulses which reach the hemispheres is that the latter are relayed in the thalamus and the former are not. In most cases the word "thalamic" can be substituted for "somatic" in fore-brain morphology. It has the advantage of being a term with a definite anatomical basis, and has no doubtful theoretical implications.

Any thorough-going criticism of Johnston's views in the basis of the work to be described in this paper will obviously be impossible, if only because of the complete lack of embryological data. It will, however, be useful to point out where in the adult anatomy observations appear to be consistent with his view, and where apparent difficulties arise.

THE OLFACTORY BULB, PEDUNCLE, NUCLEUS OLFACTORIUS ANTERIOR, AND OLFACTORY TRACTS

The olfactory bulb is an oval swelling about 1 mm. in length. It has the characteristic structure, already well described in several reptilian forms (e.g. Crosby, 1917). Glomeruli lie superficially, succeeded by a layer of mitral cells, and then by the fibres of the olfactory tracts, presumably axons of mitral cells and the granule cells which form the next layer. Inside the granule cells comes the ependyma of the olfactory ventricle, which is continuous through the peduncle with the lateral ventricle. The accessory olfactory bulb (fig. 1) extends posteriorly on the dorso-medial aspect of the peduncle for

a further millimetre or slightly more. Its structure resembles that of the olfactory bulb. In this region the tract fibres are grouped laterally and ventrally. The vomero-nasal nerves can be seen entering the accessory bulb on its medial side. Posterior to the accessory bulb is a short length of peduncle, about 0·3 mm., which contains only a ring of olfactory tract fibres superficially, a few scattered granule cells beneath them, and the olfactory ventricle.

Where it joins the hemisphere the peduncle swells out to form the nucleus olfactorius anterior (fig. 3). It is characteristically a complete ring of cells surrounding the olfactory ventricle. The cells are of medium size, and cannot be followed anteriorly into the layer of granule cells. The ring shows no differentiation at first, except that dorso-laterally the cells are rather more numerous and slightly larger, and that a little posterior to this level a similar but smaller and less definite ventro-medial accumulation can be seen. Further posteriorly this ring of cells is found to pass gradually into the various regions differentiated in the superficial parts of the hemisphere (fig. 4). Dorso-laterally it passes backwards into the pyriform cortex; dorso-medially and dorsally into the hippocampal and dorsal cortex; medially it gives place to the comparatively cell-free anterior part of the paraterminal body, while ventrally it passes into the tubercular cortex and possibly the palaeostriatum. These last two structures are too poorly differentiated from each other for this statement to be made more precise.

The fate of the olfactory tract fibres is difficult to determine, and from this material cannot be described with complete certainty. The appearances seem best interpreted in the following way. At first, in a transverse section of the peduncle, the tract fibres form a uniform superficial ring. As the nucleus olfactorius anterior is approached they accumulate among the cells in a dorso-lateral position, lying more deeply, but showing a tendency to stream towards the surface. These fibres will form the lateral olfactory tract (figs. 6, 12) superficially placed below the ventral edge of the pyriform cortex. Dorsally the fibres persist in a superficial position (fig. 18). They are least numerous here, and probably enter the dorsal part of the nucleus olfactorius anterior, although some may continue onwards to the superficial aspect of the hippocampal and dorsal cortex. Ventrally and ventro-medially fibres are fairly numerous. Many remain superficial (figs. 17, 18), and the most ventrally placed probably run on to enter the superficial surface of the tuberculum. Others become diffused among the cells of the nucleus olfactorius anterior. As the tubercular cortex and palaeostriatum begin to differentiate, fibres can be seen arranged in three zones (fig. 12): (i) superficial (fig. 12, *G*), probably tract fibres running to the tuberculum; (ii) intermediate (fig. 12, *F*), among the cells of the tuberculum, and consisting probably of tract fibres and fibres relayed in the tuberculum and on their way to the paraterminal body; (iii) deep, between the tuberculum and the palaeostriatum. This is a very mixed group of fibres and it has not been possible to analyse them with complete certainty. Some of them, probably most, are fore-brain bundle fibres on

their way to or from the striatum. These can be seen in the sagittal series (fig. 18). A few are probably either tract fibres, or tract fibres which have been relayed in the nucleus olfactorius anterior or the tuberculum. They are on their way to the paraterminal body, to the palaeostriatum, and also to an olfactory component of the anterior commissure (fig. 17), a conspicuous bundle in the lateral part of this group of fibres.

Medially the olfactory tract fibres of the peduncle preserve their superficial position. Some ascend dorsally to enter either the superficial dorso-medial surface of the nucleus olfactorius anterior or the extreme anterior end of the hippocampal cortex. Others run more directly posteriorly, are related to the nucleus olfactorius medialis (figs. 4, 20) in the anterior part of the paraterminal body, and probably end in the ventro-medial nucleus of the paraterminal body. They may reach as far as the nucleus of the diagonal band.

The lateral olfactory tract was described as coming from the dorso-lateral accumulation of cells and fibres in the nucleus olfactorius anterior. A little further posteriorly fibres can be seen entering and leaving it to and from the anterior part of the deep surface of the pyriform cortex. Its further course to the amygdaloid region will be discussed later.

This description of the olfactory tracts may be summarised as follows. After forming a complete and uniform layer round the peduncle, most of the fibres concentrate dorso-laterally, where many are no doubt relayed in the nucleus olfactorius anterior. These form the lateral olfactory tract which gives fibres to and receives them from the pyriform cortex, and connects posteriorly with the amygdaloid nuclei. Most of the remaining fibres are relayed in the nucleus olfactorius anterior which they enter superficially. They are not clearly differentiated into medial and intermediate tracts. The former is represented by fibres which run through the nucleus olfactorius medialis to the paraterminal body and possibly (but not certainly) directly to the hippocampus; the latter by fibres which run to the tuberculum, the anterior commissure (its olfactory component), and possibly to the palaeostriatum. It seems probable that the anterior part of the dorsal cortex may receive a few olfactory fibres from the dorsal aspect of the peduncle.

Discussion

It is noteworthy that the nucleus olfactorius anterior corresponds very closely with the same structure described by Herrick (1924), and the appearances fit well with his suggestions that it is a "residual undifferentiated part of a much larger area." It is clearly a secondary olfactory nucleus and many olfactory tract fibres are relayed there, although it probably serves as a correlation as well as a relay centre. Its correspondence with what Edinger, de Lange, Kappers, etc., call the "cortex of the lobus olfactorius" is obvious. In some Reptiles it is separated from the rest of the hemisphere by a "sulcus coronalis" (*Chelone imbricata*, de Lange, 1911). Commonly it extends far

forwards into intimate relation with the bulbar formation (opossum, Herrick; *Sphenodon*, Cairney), but in *Lacerta* it is separated by the comparatively cell-free peduncle. Johnston (1915), in the turtle, describes a "nucleus olfactorius anterior" which appears to be only a part of what he there calls the caudate nucleus, later (1922), the bed of the stria terminalis. As Herrick pointed out, this seems unjustified. Johnston (1915) states that both the pyriform and hippocampal formations reach forwards into close contact with the "olfactory formation," and in doing so he is probably referring to Herrick's nucleus olfactorius anterior. Crosby (1917) describes an anterior olfactory nucleus in the alligator. In her fig. 3 (p. 390) this appears as a collection of cells lying ventrally in the peduncle and forming part of a cortical ring similar to that described here for *Lacerta*. The ring shows more differentiation, so that she is able to distinguish the hippocampal from the pyriform part of it. It is possible that here is a nucleus olfactorius anterior which differs from that of *Lacerta* only in its degree of differentiation, or that sections a little further forward would have shown a condition quite like that in *Lacerta*. It appears then, that a nucleus olfactorius anterior is very generally present in Reptiles, and that it is very like the same structure described in the lower Mammals by Herrick (1924), Le Gros Clark (1928), and others.

In *Lacerta* the lateral olfactory tract is much the largest and most definite of the olfactory tracts. In this it agrees with the descriptions published of other forms. Its connections with the nucleus olfactorius anterior, the pyriform cortex, the nucleus of the lateral olfactory tract, and the amygdaloid nuclei are remarkably constant throughout the class. How much of the tract is relayed in the nucleus olfactorius anterior it is impossible to say. It is certain that, as the tract runs posteriorly, it comes to contain fewer secondary and more tertiary fibres. It seems best, nevertheless, to keep the term "lateral olfactory tract," remembering this constant loss of secondary and gain of tertiary fibres, rather than the terms "tractus bulbo-corticalis" and "tractus cortico-epistriaticus" introduced by Edinger, since both the latter involve assumptions which cannot yet be proved.

The medial and intermediate tracts are small and difficult to follow. There appears to be no doubt about their connection in all the described forms with the tuberculum and paraterminal body, or about the presence of a connection in the anterior commissure from the intermediate tract, although the last is not mentioned by Cairney for *Sphenodon*. A direct connection with the anterior part of the hippocampal cortex is described by P. Ramón y Cajal (1917). The evidence from my material is not definite. The presence of an olfactory tract connection with the medial part of the palaeostriatum (called by Johnston the nucleus caudatus in 1915 and bed of the stria terminalis in 1923, and by Cairney, Herrick and others olfacto-striatum) is also suggested but not definitely proved by my material. Cairney describes it definitely in *Sphenodon*. This is a point of some importance since the justification of the name "olfacto-striatum," a useful one in many respects, depends upon it. It is a point which deserves

further investigation. Another question which remains to be decided is whether intermediate olfactory tract fibres run down with the mediate fore-brain bundle to the hypothalamus and mid-brain, as Herrick (1924) says they do in the opossum.

TUBERCULUM OLFACTORIUM

In *Lacerta* this structure is characterised by its poor differentiation and its lack of clear boundaries. It lies (figs. 1, 20) in the base of the brain between the nucleus olfactorius anterior in front and the fibres of the diagonal band behind. Medially it reaches up to the paraterminal body (figs. 5, 6), and laterally to the lateral olfactory tract and the endorhinal fissure. It lies superficial to the palaeostriatum.

It consists of small cells among which are scattered a few fairly large polygonal cells. Their arrangement is hardly definite enough to merit the term "cortex." It is only distinguishable as such where it is separated from the palaeostriatum by fibres of the medial fore-brain bundle, the olfactory tracts, and the olfactory component of the anterior commissure. This region is shown in fig. 6 as a cell-free zone between the tuberculum and the palaeostriatum. Anteriorly it blends with the nucleus olfactorius anterior. Laterally it is indistinguishable from the underlying palaeostriatum (fig. 6), and it is indeed doubtful whether this lateral part should be included in the tuberculum at all. It contains fibres of the lateral fore-brain bundle (fig. 12), and may represent the region which Johnston (1922) calls the anterior perforated space. It also lies in the position of the nucleus of the lateral olfactory tract (turtle, Johnston, 1915), but appears to receive no, or very few, olfactory tract fibres.

Medially and anteriorly there is a small nucleus of round cells in the anterior part of the medial hemisphere wall, which will be called the nucleus olfactorius medialis (figs. 4, 20); some of the fibres of the medial olfactory tract pass through it. As it is probably a cell station in the path of fibres afferent to the hippocampus, it is best included in the paraterminal body, although, as olfactory fibres are also relayed in the tuberculum on their way to the hippocampus, there are as good reasons for calling it a specialised part of the tuberculum.

The fibres related to the tuberculum are very diffusely arranged, so that an exact analysis is not possible in this material. Olfactory tract fibres appear to enter it superficially (figs. 12, *G*, 17). In its substance numerous fibres can be seen, all with a dorso-medial inclination, probably running to the paraterminal body and hippocampus (fig. 12, *F*).

Other fibre tracts related to the tuberculum may of course be connected with it. Such tracts are: the diagonal band posteriorly, the anterior olfactohabenular tract superficial to it (fig. 12) and the fore-brain bundles and olfactory component of the anterior commissure (fig. 12) deep to it. Definite evidence of connections with these tracts cannot be obtained from my material.

Discussion

The area which has been described here as the tuberculum olfactorium corresponds with the basal olfactory area of Selachians (see Johnston, 1922). In this area in Reptiles and Mammals Johnston differentiates not only a tuberculum, but also an "anterior perforated space." The degree of differentiation in *Lacerta* does not seem to justify such a subdivision of the area in question, although it is possible that its lateral part, where it is practically indistinguishable from the underlying palaeostriatum (fig. 6), represents Johnston's anterior perforated space. Differentiation of a cortex in the tuberculum appears to be much more definite in some other reptilian forms. Johnston (1915), for the turtle, describes a double cortical layer in the deep part of which islets of Calleja can be seen. Crosby (1917), in the alligator, also describes a deep and superficial part, while Durward (1930), in his figures of *Sphenodon*, shows a much more clearly differentiated cortex than is present in *Lacerta*.

A considerable amount of confusion in the terminology of this region has been introduced by the use of such terms as "area olfactoria" and "area parolfactoria," chiefly by Edinger and other continental writers. With regard to the term "parolfactory" Prof. Elliot Smith has kindly allowed me to see some notes of his own about its history. It was first used by His as a substitute for "Broca's area," when eponymous terms were being eliminated in the development of the B.N.A. terminology. Unfortunately he applied it to a small area of neopallium anterior to the paraterminal body, the area defined by Broca in the donkey's brain. Edinger introduced more confusion by including the tuberculum olfactorium in his "area parolfactoria." Most subsequent writers have used the term without any strict definition, and it seems needless to say more than this as a justification for dropping it altogether.

Descriptions of the connections of the tuberculum for different forms agree very well among themselves and with the observations recorded here. The fibres running from it to the paraterminal body and hippocampus have been variously described as "tuberculo-cortical," "tuberculo-septal," "septo-parolfactory," etc. The anterior olfacto-habenular tract has been very generally described (e.g. Cairney, *Sphenodon*; de Lange, *Varanus*, etc.) as connected to the tuberculum and also the olfactory component of the anterior commissure. Although these connections very possibly exist in *Lacerta*, the evidence for their presence is not conclusive.

VENTRO-LATERAL REGION

General

This is a well-developed and important region in the reptilian fore-brain. It includes the corpus striatum and the amygdaloid nuclei, both "basal" structures. The pyriform cortex, because of its connection to the lateral olfactory tract, its relation to the amygdaloid nuclei (Johnston, 1922), and its development and position below a zona limitans lateralis (Johnston, 1916 *b*),

might reasonably be included as well. This is Johnston's view. The embryological findings on which it is based are not extensive and not entirely convincing, and other observers, e.g. Herrick (1910), have come to different conclusions. The pyriform cortex seems to be a structure which has relationships to both the ill-defined "pallial" and "basal" regions of the hemisphere wall, and it is impossible to place it completely in one or the other. While recognising its relationship to "basal" structures, it will be described here with the other cortical or pallial areas.

Owing to the complexity of this region and the difficulty in finding obvious homologies for its differentiated parts, a large and confusing nomenclature has grown up around it. It cannot easily be delimited on the outer surface of the brain because its most characteristic feature is its growth into the ventricular cavity, but it corresponds roughly with the region below the endorhinal fissure (fig. 1), deep to the tuberculum olfactorium. It is seen best in transverse section (figs. 4–10) and also in a parasagittal section (fig. 11), as an enormously thickened part of the hemisphere wall, which forms a very conspicuous prominence in the lateral ventricle. This prominence has been given various names. It is not a simple structure, so that names like "hypopallial ridge," "epistriatum," and so on, which have been applied to it, should not be used for the prominence as a whole. Johnston's term, "dorsal ventricular ridge," applies only to a part of it. Elliot Smith (1919) pointed out that it was first observed and noted by John Hunter, and in one of his figures (fig. 14, p. 282) he labels it "Hunter's eminence." This seems a very appropriate term to use for the structure as a whole.

The main constituents of this ventro-lateral region and of Hunter's eminence are shown clearly in figs. 5 and 6, which are transverse sections of the hemisphere nearer its anterior than its posterior end. The greater part of Hunter's eminence is occupied by the "hypopallium" (Elliot Smith, 1919). Beneath the hypopallium and in the basal part of the ridge is a large mass of cells, the palaeostriatum. It surrounds the ventral angle of the ventricle and abuts on the paraterminal body medially. Laterally it is separated from the hypopallium by a cell-free zone in which many blood vessels can be seen (lateral striate arteries, Elliot Smith, 1919) (fig. 5). It is covered ventrally by the ill-defined cortex of the tuberculum. Posteriorly the ventro-lateral region is rather differently constituted, and the main features can best be seen in the parasagittal section (fig. 11). The hypopallium occupies the whole of the ventricular surface of Hunter's eminence, but its posterior part is sharply differentiated from the anterior at the point *B*. This differentiation of anterior and posterior parts in the hypopallium was noted by Dart (1920), who called them hypopallium anterior and posterior respectively. These terms were adopted by Cairney and Durward for *Sphenodon*, and will be used here, although it seems doubtful if the two parts are as closely related as the terms imply. The hypopallium posterior corresponds with Kappers' "archistriatum," and in part at least with Edinger's "epistriatum," but neither of these terms is

appropriate. For various reasons, the chief of which is its connection with the lateral olfactory tract, it should be included in the amygdaloid and not in the striatal complex.

The remaining part of the amygdaloid complex occupies the basal part of Hunter's eminence, corresponding in position to the palaeostriatum which lies in front of it. It can be seen in fig. 11 (*Amy.*), lying just behind the palaeostriatum, from which it is not very clearly differentiated.

The most conspicuous and characteristic fibre tracts of the ventro-lateral region are the fore-brain bundles, the lateral olfactory tract, and the anterior commissure. The fore-brain bundles connect predominantly with the palaeostriatum and the hypopallium anterior, and the lateral olfactory tract with the amygdaloid complex (including the hypopallium posterior). The anterior commissure contains fibres which connect with all the parts of this region.

The palaeostriatum

This is a mass of cells which extends from between the planes of figs. 4 and 5 anteriorly, where it is hardly distinguishable from the deep part of the tuberculum and the nucleus olfactorius anterior, back to the level of the commissures (fig. 9), where it ends in some scattered cells around the anterior commissure, among the fibres of the fore-brain bundles (fig. 14), and by blending to some extent with the amygdaloid complex dorsal to the fore-brain bundles (fig. 9, *C*). It is covered ventrally and anteriorly by the tubercular cortex, and posteriorly by the fibres of the diagonal band (fig. 13).

The main relations of the palaeostriatum to the other cell masses can be seen in figs. 5–8. That part which encroaches on the medial hemisphere wall below the paraterminal body (well seen in fig. 5) has frequently been given a separate name, the "nucleus accumbens" (Ziehen, Herrick, etc.). There is some indication of a division of the palaeostriatum into medial and lateral parts (figs. 5, 6), the lateral consisting of rather larger cells than the medial. These parts clearly correspond with the olfacto-striatum (medial) and the so-called "somatic-striatum" (lateral) of Cairney, Durward and others. For a short part of its extent the palaeostriatum is separated by rather indefinite ventricular sulci from the paraterminal body medially and the hypopallium laterally (figs. 5, 6).

About the level of the commissures a few cells of fairly large size can be seen among the fibres of the stria terminalis. They are shown in fig. 11 between the palaeostriatum and the amygdaloid and less definitely in fig. 9, *C*, dorsal to the fore-brain bundle. It is difficult to say whether these belong to the amygdaloid or to the palaeostriatum.

The chief connections of the palaeostriatum are with the fore-brain bundles. Anteriorly, between it and the tuberculum, fibres of the medial fore-brain bundle can be seen (figs. 12, 18). Some of these appear to begin or end in the medial part of the palaeostriatum (olfacto-striatum) although most are connected to the paraterminal body. In the same region olfactory tract fibres and

the olfactory component of the anterior commissure may connect with the palaeostriatum. Laterally it is occupied by the dense network of fibres of the lateral fore-brain bundle (fig. 12). Many of these are on their way to the hypopallium anterior or dorsal cortex, but many no doubt end or begin in the lateral part of the palaeostriatum. Through the fore-brain bundles the palaeostriatum is connected with the thalamus, hypothalamus, mid-brain, and possibly lower levels of the nervous system, and both bundles probably contain ascending and descending fibres.

The hypopallium anterior

This structure can be seen in figs. 4–7 in the transverse series, and throughout its whole antero-posterior extent in fig. 11. It forms the greater part of the ventricular surface of Hunter's eminence, and consists of a fairly definite layer of cells beneath the ventricular ependyma, limited ventrally and medially by a sulcus which separates it from the palaeostriatum. This layer is particularly definite medially and anteriorly, but everywhere there is a marked tendency to the formation of clumps of cells. Laterally and anteriorly (fig. 4) it is continuous for a short distance with the dorsal cortex, underneath the pyriform cortex. Behind the level it is in intimate contact with the ventral edge of the pyriform (figs. 5, 6), and in most sections appears to be continuous with it. Inside the cup formed by the cell layer beneath the ependyma is a core containing fewer and smaller cells. Posteriorly cells of the hypopallium anterior extend back on either side of the hypopallium posterior. These two extensions can be seen in figs. 8 and 9 (*Hyp. ant.*).

Its dorsal limit posteriorly is marked by a very slight depression (fig. 11, *B*) on the ventricular surface of Hunter's eminence. The notch marked *A* in the same figure is probably an artefact. It can be seen only in about six consecutive sections and only in the one series. The ill-defined sulcus *B* corresponds with Kappers' "sulcus neo-archistriaticus" or de Lange's "sulcus striato-epistriaticus," which is apparently very well marked in *Varanus* and some snakes.

The main connection of the hypopallium anterior is with the lateral fore-brain bundle. Its fibres radiate in the core of the hypopallium to all parts of the layer of cells beneath the ependyma (fig. 12). These fibres connect it with the thalamus, and possibly the hypothalamus and mid-brain. Among them may be short fibres between the hypopallium and palaeostriatum as well. Fibres from the hypopallium anterior also form a large component of the anterior commissure (fig. 14). They appear to connect with the hypopallium and amygdaloid complex of the opposite side.

The amygdaloid complex

This is a region of the reptilian brain which it is exceedingly difficult to describe clearly and in such terms as facilitate comparison with the published descriptions of other forms. These descriptions all show a general agreement in

that they place the region in question in the hinder part of the ventro-lateral area, and describe its main connections with the lateral olfactory tract, the anterior commissure and the stria terminalis. In terminology there is practically no agreement between any two workers, and the more detailed the analysis, the greater the confusion has become. Johnston's attempt (1922) to reduce this confusion to some sort of order is the most thoroughgoing and consistent, but suffers from the defect, as far as Reptiles are concerned, that it depends for this class on a detailed description of only two forms, the turtle, investigated by himself in 1915, and the alligator, described by Crosby in 1917. It is difficult to compare the condition in *Lacerta* directly either with the turtle or the alligator, so that one is left in the dilemma of adding to an already too complicated terminology or of using terms which imply uncertain homologies, and have been used in many different ways. As a compromise as few specific terms as possible will be used, and only those implying general homologies which are reasonably certain.

The amygdaloid complex of *Lacerta* consists of two main parts, the hypopallium posterior, and a less well-defined structure, which will be called the "central amygdaloid mass." This latter term is not meant to imply an homology with Johnston's "central amygdaloid nucleus," although it is probable that in other animals the central and other amygdaloid nuclei described by Johnston have differentiated in the region of my "central mass." The two parts can be seen in fig. 11. The central mass (*Amy.*) lies behind the palaeostriatum, with which it is more or less continuous, below the hypopallium anterior. It is superficial ventro-laterally behind the tuberculum olfactorium. The hypopallium posterior lies behind the central mass, and its general relations can be seen in the figure.

In fig. 6 a few cells scattered among the fibres of the lateral olfactory tract can be seen (*Tr. olf. lat.*). These probably represent the nucleus of the lateral olfactory tract. They are continuous with the central amygdaloid mass behind, and their degree of differentiation in *Lacerta* does not seem to justify a separate name. In fig. 7 the central mass can be seen below the endorhinal fissure and above the lateral fore-brain bundle, separated from the latter by a blood vessel. The lateral olfactory tract lies in the middle of it. It reaches its maximum development about the level of the commissures (figs. 8, 9). In these figures, on account of the obliquity of the sections (see fig. 2 *a*), the hypopallium posterior has begun to appear above the central mass. It is not clearly differentiated from the central mass ventrally.

The hypopallium posterior has a very characteristic cup-like form, the mouth of the cup being open ventrally and anteriorly, and the rim more or less fused with the central amygdaloid mass. Its general form and relations can be seen in figs. 8–11. Its continuity with the pyriform cortex laterally can be seen in fig. 10.

The principal connections of the amygdaloid complex can be classified in three groups: olfactory, commissural, and hypothalamic. With the latter may

be included preoptic connections. There are in addition important but less conspicuous connections with the diagonal band and the stria medullaris.

Olfactory impulses arrive *via* the lateral olfactory tract from the bulb, nucleus olfactorius anterior, and probably the pyriform cortex. The tract is at first superficial, just below the endorhinal fissure (figs. 6, 12). It soon leaves the surface and runs through the central amygdaloid mass (figs. 7, 13–15), becoming a much less compact bundle. No doubt many of its fibres end here. Other fibres leave the main tract and turn ventrally into the basal part of the central amygdaloid mass (figs. 9, 11, and 15, *C*). The remaining fibres can be traced onwards as a very diffuse bundle into the concavity of the cup-like hypopallium posterior (fig. 16).

Hypothalamic connections (the olfactory projection tract of Cajal). These are a well-developed but rather diffuse bundle of fibres seen best in fig. 15 (*St. term.*). They arise for the most part in the medial and ventral parts of the central amygdaloid mass, and sweep medially and ventrally over the fore-brain bundles into the hypothalamus. Some join the fore-brain bundles and probably reach the hypothalamus at a more posterior level. Scattered among their fibres are the cells mentioned above (p. 170) and seen in fig. 9, *C*.

Preoptic connections. There is another bundle (fig. 13, *Amy. preop.*) which connects the anterior end of the central amygdaloid mass with the preoptic nucleus. It runs outside and below the fore-brain bundles, and it is possible that some of its fibres run on to the paraterminal body and the hippocampus. They appear to end in the preoptic region however.

Commissural connections. These all run in the anterior commissure, chiefly in what is called here its amygdaloid component. This arises as a large bundle of fibres from the central mass of the amygdaloid (best seen in fig. 14). It is joined by the olfactory component (fig. 17) and crosses in the anterior part of the commissure (fig. 18). It appears to be distributed to the hippocampus and the hypopallium anterior and posterior of the opposite side, but this cannot be stated with certainty from this material. Commissural fibres from the posterior part of the central amygdaloid mass and from the hypopallium posterior join what is called here the hypopallial component of the anterior commissure. This can be seen in figs. 14–16, and in transverse section in figs. 17 and 18. It forms the dorsal and posterior part of the anterior commissure. It is possible that some of the fibres which run forwards from the posterior parts of the amygdaloid in this component are not commissural, but connect with the paraterminal body above and below the commissure (cf. Johnston, 1922, p. 397). The commissural fibres appear to connect with the same regions of the opposite side.

The diagonal band is seen in fig. 13 (*D.B.*) and again in figs. 17–19. Its fibres arise chiefly from the anterior part of the central amygdaloid mass and superficial to the lateral olfactory tract. A few probably originate in the pyriform cortex. They run ventrally and then turn medially below the fore-brain bundles and behind the tuberculum (fig. 13). They then ascend through

the nucleus of the diagonal band (figs. 8, 20, *N.D.B.*), where they are perhaps relayed, and sweep dorsally anterior to the commissures and turn posteriorly above them (fig. 19). They are cut transversely as they run posteriorly in figs. 13–15. Some of these fibres enter the tangential system of fibres superficial to the hippocampus (fig. 14) and probably the bundle as a whole is afferent to the hippocampus. Some of its fibres may connect with the cells of the nucleus of the hippocampal commissure (fig. 20, *N. com. hip.*), most enter the supraforaminal part of the paraterminal body, while others may connect with the ventro-medial nucleus of the paraterminal body further forwards.

The connection to the habenula consists of a few fibres from the ventral part of the central mass which join the stria medullaris lateralis as it lies in the angle between the optic tract and the fore-brain bundles (fig. 15, *St. med. lat.*); the actual amygdaloid connection was not visible in the section from which this figure was drawn. A few fibres from the medial part of the central mass run to the medial cortico-habenular tract (fig. 17, *Amy. hab.*).

It would be well at this point to summarise the main facts about the amygdaloid complex and its connections.

The amygdaloid consists of two main parts, a central mass and the hypopallium posterior. The central mass shows a fairly well-marked ventral condensation of cells which extends back beneath the hypopallium posterior (fig. 11, *C*). This ventral condensation receives a special bundle from the lateral olfactory tract, gives rise to the greater part of the olfactory projection tract to the hypothalamus, and is not easily distinguishable from the palaeostriatum which lies in front of it. It has a small habenular connection.

Commissural fibres run from or to all parts of the amygdaloid; anteriorly these fibres form a large "amygdaloid component" of the anterior commissure, while posteriorly they join the "hypopallial component."

Besides giving the special bundle mentioned above, the lateral olfactory tract brings olfactory impulses to all parts of the amygdaloid.

The diagonal band connects the anterior and lateral part of the central mass with the medial olfactory centres, and this same region of the amygdaloid has a small bundle of fibres running below the fore-brain bundles to the preoptic region. It is probable that this anterior and lateral part of the central mass is the representative of the nucleus of the lateral olfactory tract which is better differentiated in other reptilian orders.

Discussion

Herrick (1921) has described the main features of the ventro-lateral region of the brain wall in Amphibia. In the urodeles there is an undifferentiated strio-amygdaloid mass, having many of the connections typical of the striatum and amygdaloid, but not yet clearly marked off as separate tracts. Differentiation has proceeded much further in the Anura which show a condition in many ways comparable to the Reptiles. Anteriorly is a corpus striatum (or

palaeostriatum), while posteriorly and bulging into the ventricle at the level of the foramen of Monro is the amygdaloid nucleus. This amygdaloid nucleus receives a separate division of the lateral olfactory tract (Herrick's ventro-lateral olfactory tract) from the vomero-nasal organ of Jacobson. A dorso-lateral division of the tract runs to the rudimentary pyriform cortex. The corpus striatum, Herrick states, is dominated by somaesthetic impulses from the thalamus, and has been almost entirely freed from olfactory connections. He derives the whole lateral wall of the amphibian hemisphere from the lateral olfactory area of lower Vertebrates, and divides it in Amphibia into dorso-lateral (pyriform) and ventro-lateral (strio-amygdaloid) regions. These two divisions are separated by his zona limitans lateralis. In this he disagrees with Johnston (1922), who places his zona limitans above the pyriform cortex. The modern Amphibia are very specialised animals, and it seems possible that the clear subdivision of the lateral region of the amphibian hemisphere into dorso-lateral and ventro-lateral parts, each with its own division of the lateral olfactory tract, may be a specialisation, and not of fundamental importance in fore-brain morphology. The facts suggest that the attempt to find a definite zona limitans, valid for all groups and separating "pallial" from "basal" areas, is vain, especially, as Herrick points out, in the absence of precise definition of the terms "pallial" and "basal."

There is, however, no doubt that the palaeostriatum and amygdaloid nucleus of Anura correspond very closely to the structures given those names here in *Lacerta*. That the correspondence applies to fibre connections as well as to topographical position can be verified by reference to Herrick's paper (1921).

Among the Reptiles themselves the first point for discussion concerns the medial part of the palaeostriatum, which lies beneath the praterminal body in the medial hemisphere wall. This cell mass has been included in the praterminal body or "septum" by several authors, notably Herrick, under the name of "nucleus accumbens." It has been pointed out many times (e.g. by Johnston, Kappers, Cairney) that this nucleus accumbens is far more closely related to the palaeostriatum than to the praterminal body. In fact, the only reason for separating it seems to be an adherence to an artificially rigid subdivision of the hemisphere into ventro-medial and ventro-lateral parts. From its cell type and fibre connections it appears to belong to the striatum, and, as this is generally recognised, it seems best to include it under the term "palaeostriatum" and to drop the term "nucleus accumbens" altogether. For the palaeostriatum to be indented from above by the lateral ventricle seems to be typical not only of Reptiles, but of Amphibia and Mammalia as well.

An important point is the division of the palaeostriatum into medial and lateral parts. The evidence of this from cell-stained preparations alone is not very good in *Lacerta*. In the fibre-stained series, however, it is conspicuous that the medial part is connected mainly with the hypothalamus by the medial fore-brain bundle, and possibly with the olfactory tracts, and that the lateral part has strong thalamic connections *via* the lateral fore-brain bundle. These

parts clearly correspond with the olfacto-striatum and "somatic" striatum of Cairney and Durward, and with the bed of the stria terminalis and the putamen of Johnston (1922). Johnston looks upon the bed of the stria terminalis as primarily an olfactory centre derived from the deep or ventricular part of the lateral olfactory area of Selachians. The term "olfacto-striatum" also implies an olfactory origin. Unfortunately, no very clear evidence of olfactory connections in this region was obtained in *Lacerta*. Herrick, too, in Amphibia, states that direct olfactory connections to the palaeostriatum are few or absent. In *Sphenodon* Cairney has described olfactory tract fibres running to the olfacto-striatum, so that in view of the equivocal evidence of *Lacerta*, the point deserves further investigation. The study of degeneration following experimental lesions probably offers the best hope of definite results.

Johnston's term, "bed of the stria terminalis," for this structure seems to have no particular advantage over "olfacto-striatum," and in some ways is less appropriate. The greater part of it lies anteriorly in the hemisphere where there are no fibres of the stria terminalis, unless those fibres of the medial fore-brain bundle which connect it with the hypothalamus are included in that system. In Reptiles at least it is a primary division of the palaeostriatum and as such is well described by the term "olfacto-striatum."

The identity of the lateral part of the palaeostriatum of *Lacerta* with the "somatic" striatum in *Sphenodon* (Cairney, Durward) and with the putamen in the turtle (Johnston, 1922), seems to be quite clear. In *Lacerta* it is pierced by fibres connecting the thalamus with the lateral edge of the dorsal cortex similar to those Johnston has described for the turtle. From Crosby's (1917) description of the alligator there again seems no doubt that the palaeostriatum is divided into the same two parts, medial and lateral, called by her ventro-lateral small- and large-celled areas respectively. It may be said then, that a palaeostriatum divided into medial and lateral parts is characteristic of the Reptiles as a whole, that the medial part is primarily concerned with olfactory impulses, and the lateral with sensory impulses which reach it by way of the thalamus.

Johnston, in describing the olfacto-striatum as the bed of the stria terminalis, states that posteriorly it runs more or less indistinguishably into the central and medial amygdaloid nuclei, and that it forms the bed of the anterior commissure. In *Lacerta* the distinction between this part of the palaeostriatum and the central mass of the amygdaloid is certainly difficult to make out, and it appears that the few cells scattered around the anterior commissure belong rather to the striatal than to the paraterminal region. Cairney and Durward both describe the olfacto-striatum as distinguishable from the amygdaloid nuclei. So far as it goes, my material supports Johnston's view.

THE HYPOPALLIUM ANTERIOR AND POSTERIOR

Although these two structures are essentially distinct, at least in *Lacerta*, they have been very generally described together. The term "hypopallium" was introduced in 1919 by Elliot Smith to describe the whole of the cortex-like arrangement of cells on the ventricular surface of Hunter's eminence, or the "hypopallial eminence" of his paper. This ridge, as is shown in his fig. 5, p. 275, extends "from the extreme anterior end to the posterior inferior recess of the hemisphere." In the sections which he shows (*ibid.* fig. 6, p. 276) it can be seen that the layer of cells in the extreme posterior end of the ridge is broken into clumps, a fact noted by Dart (1920), who consequently divided the hypopallium into hypopallium anterior and hypopallium posterior. Cairney (1926) further noted that the hypopallium posterior had connections with the lateral olfactory tract. Durward (1930) divided the hypopallium differently. According to him, only that part which is in contact with the dorsal cortex should be called hypopallium anterior, while all the rest, in contact with the pyriform cortex, is hypopallium posterior. The morphological value of these apparent connections between cortical and hypopallial areas has been questioned (Hines, 1923); the difference in the fibre connections anteriorly and posteriorly is quite definite and is a much more fundamental distinction, and one about the value of which there is no disagreement. It seems therefore best to keep the term "hypopallium posterior" for that part of the hypopallium which has connections to the lateral olfactory tract. Crosby found similar olfactory connections for the posterior part of the hypopallium, her "dorso-lateral area." Johnston looks upon the whole of his dorsal ventricular ridge as hypopallial, presumably hypopallium anterior. The hypopallium posterior is the "amygdaloid ridge" of Johnston's paper (1922) or the posterior end of the "dorsal ventricular ridge" (1915). It is well shown by Elliot Smith in his fig. 14 (1919).

It appears then, that at the posterior end of Hunter's eminence there is a region connected with the lateral olfactory tract. In *Sphenodon* and the alligator this region is not well developed and not very clearly differentiated from the anterior part of the eminence. In the turtle it is still small, but can be clearly differentiated. In *Lacerta* it forms a well-developed and clearly differentiated structure, the hypopallium posterior. In *Varanus* and some snakes (de Lange, 1911) it is even more conspicuous and may be separated from the anterior part of Hunter's eminence by a sulcus, the "sulcus neo-archi-striaticus" of Kappers. In addition to the names already mentioned for this structure, it has been called the "nucleus sphaericus" (Meyer) and the "nucleus occipito-basalis" (C. L. Herrick). Because of its connection with the lateral olfactory tract and its position in the hemisphere wall, it is now generally agreed that the hypopallium posterior should be included in the amygdaloid complex. Because it reaches its greatest development in such specialised orders as the Lacertilia and Ophidia, it seems possible that it is a structure

which is peculiar to the Reptiles and that no exact homologue will be found in the mammalian amygdala. Dart (1920) homologises it very confidently, but on little concrete evidence, with what he calls the "element C" of the mammalian amygdaloid complex. This "element C" is the "nucleus amygdalae" of Winkler and Potter, and appears to be the lateral amygdaloid nucleus of Johnston (1922). The position under the ependyma of the lateral ventricle (well shown in some of Johnston's figures) does suggest a comparison with the hypopallium posterior of Reptiles, but more detailed knowledge of fibre connections and development is necessary before definite statements can be made on this point. Dart says (p. 21) that this hypopallium posterior discharges by a tractus hypopallio-habenularis to the habenula. Cairney does not mention this connection, and there is no sign of it in *Lacerta viridis*. Possibly he is referring to the connection between the central mass of the amygdaloid and the habenula. Dart's one figure which shows this tract is not clear enough to help in deciding this.

The relationship of the hypopallium anterior and posterior to the dorsal cortex and pyriform cortex is striking and important. So far as adult appearances go, in *Lacerta viridis* one can say that the extreme anterior end of the hypopallium is in intimate contact with the dorsal cortex where it bends ventrally under the pyriform, a region called by Elliot Smith (1919) the "primordium neopallii." For the greater part of its extent, however, the hypopallium anterior is apparently continuous with the ventral edge of the pyriform cortex, as is also the hypopallium posterior. These appearances suggest, as Elliot Smith pointed out, that the hypopallium (both anterior and posterior parts) has been formed by a growth inwards from, or an involution of, the ventral edge of the pyriform cortex. In Chelonia, however, there is a more extensive relationship between the dorsal cortex and the anterior part of the hypopallium anterior than in Lacertilia or in *Sphenodon*. A study of the adult relationships (1915) and of the embryology (1916 *b*) of this region in turtles led Johnston to the conclusion that the dorsal ventricular ridge or hypopallium anterior developed in this animal from the ventral edge of the dorsal cortex. He suggests further (1922) that only the posterior end of Hunter's eminence, the hypopallium posterior or the amygdaloid ridge, develops from the ventral edge of the pyriform, although he has not been able to observe the steps in this development owing to a lack of embryos of a suitable age. In short, the hypopallium anterior is developed from the ventral edge of the dorsal cortex, the hypopallium posterior from the ventral edge of the pyriform, and any connection between the hypopallium anterior and pyriform seen in the adult must be secondary. Hines (1923), working on *Sphenodon*, concluded that the hypopallium developed *in situ* and that all adult cortical connections were secondary. Hines' material was admittedly not entirely satisfactory, and an important part of Johnston's account is hypothetical. It is also clear that an apparent cellular continuity between the hypopallium and a cortical area in the adult is not sufficient evidence for deriving one part with certainty from the other. From what is

known of the embryology in *Sphenodon* and the turtle, it seems likely that a considerable part of the hypopallium is not derived ontogenetically from the pyriform, and that it may be derived from the dorsal cortex, or may develop *in situ*. Obviously a very much more detailed knowledge of the embryology of this region in the different orders of Reptiles is necessary before more positive statements can be made.

There remains the central mass of the amygdaloid. Its main characteristics are that it lies behind the palaeostriatum, from which it is poorly differentiated, and that it gives rise to the greater part of the amygdalo-hypothalamic fibres (olfactory projection tract of Cajal, "bundle 2" of stria terminalis of Johnston). Although differentiation in this mass is not clear enough for it to be possible to subdivide it with any certainty, in the characteristics mentioned it corresponds very closely with Johnston's medial and central amygdaloid nuclei. For the same reasons it corresponds with Durward's and Cairney's anterior amygdaloid nucleus in *Sphenodon*, and with Crosby's nucleus ventro-medialis in the alligator. Several related nuclei have been described by these workers. The nucleus of the lateral olfactory tract has been described by Johnston, Crosby, Cairney and Durward as closely related to or continuous with the amygdaloid nucleus in question. So far as there is a nucleus of the lateral olfactory tract in *Lacerta*, it is the anterior prolongation of the central mass along the lateral olfactory tract, which corresponds in every way to the nucleus described by the above-mentioned workers.

There is a nucleus in the turtle which Johnston described in 1915 as the "medial amygdaloid nucleus" and in 1922 as the "basal amygdaloid nucleus." This Cairney (1926) homologises with the posterior amygdaloid nucleus of *Sphenodon*. A clearly differentiated comparable region does not exist in *Lacerta*, but it may be represented by the condensation of cells beneath the hypopallium posterior (fig. 11).

Crosby mentions an "intermedio-lateral area," closely related to the nucleus of the lateral olfactory tract and to the posterior part of the hypopallium (dorso-lateral area, Crosby). There is no representative of this area in *Lacerta*, and apparently none in Chelonia or in *Sphenodon*. From Crosby's account it would be reasonable to include it in the amygdaloid complex together with the hypopallium posterior, but the available facts do not justify a more definite statement. Shanklin (1930) describes a similar area in the chameleon, but classes it with the palaeostriatal centres.

The terminology which has been used so far is chiefly that of Elliot Smith, but is not very different from that used by most American workers. The continental workers, led by Edinger and Kappers, have used different terms, about which a word must be said. Edinger (1908) describes this ventro-lateral region of the fore-brain as the "Stamm-lappen," and includes in it an "epistriatum" and a "palaeostriatum," present from Fishes upwards. He states that the epistriatum is characterised by its lateral olfactory connection, the tractus cortico-epistriaticus, and by olfactory connections *via* the anterior

commissure, and that it is also connected with the stria terminalis and is homologous with the amygdala of Mammals. From this it follows that his epistriatum must include the hypopallium posterior and also the central amygdaloid mass. From his figures, however (e.g. fig. 247, p. 277), it is clear that he includes the hypopallium anterior in the epistriatum. The objections to this are obvious. The hypopallium anterior has none of the connections which Edinger himself mentions as characteristic of the epistriatum. Two figures which he gives of sections through the chelonian brain complicate the account still more (fig. 247, p. 277; fig. 279, p. 309). Above a basal striatum (=palaeostriatum) are two ventricular ridges, labelled "mesostriatum" and "epistriatum" respectively. De Lange (1911) states that these two structures are both epistriatal, but comparison with Johnston's fig. 22 (1915, p. 445) suggests that the upper is the "pallial thickening" (Elliot Smith's "primordium neopallii") and the lower, Edinger's "mesostriatum," only the anterior end of the dorsal ventricular ridge or hypopallium anterior. De Lange (1911) has further confused the matter by using the term "epistriatum" for both anterior and posterior parts of the hypopallium in Chelonia, and for the posterior hypopallium alone in Lacertilia and Ophidia, although he has not been quite consistent even in this. His fig. 43, from *Lacerta*, labels what is clearly hypopallium anterior as "epistriatum." More detailed criticism of de Lange's terminology, and particularly his misuse of the term "neostriatum," is given by Elliot Smith (1919) and Johnston (1922), and is unnecessary here. The use of the term "epistriatum" has, however, been continued by Kappers (1929). He applies it to an ill-defined part of the strio-amygdaloid complex of fishes and Amphibia which receives secondary olfactory fibres, and to the nucleus of the lateral olfactory tract of Reptiles. The justification for this use of a term which has already had several different meanings attached to it does not seem to be very great. The figures which de Lange and Kappers give of the "epistriatum" in Amphibia do not show it as a structure at all clearly differentiated. The only structure clearly differentiated in the ventro-lateral hemisphere wall, and receiving olfactory tract fibres, is the amygdaloid nucleus described and figured by Herrick (1921) for the frog. From its position and connections, this amygdaloid would correspond very closely with the central amygdaloid mass, and is probably the representative of the whole amygdaloid complex. The nucleus of the lateral olfactory tract in Reptiles is a collection of cells which retains a simple connection with and arrangement among the fibres of the lateral olfactory tract. There seems no reason why it should be considered to be the representative of all that part of the ventro-lateral brain wall which receives impulses from the lateral olfactory tract in Amphibia. To the hypopallium anterior and posterior Kappers has given the names "neostriatum" and "archistriatum." Since very little is known of the relative phylogenetic age of these two parts, and since what evidence there is points rather to a pallial than striatal origin, it seems better to keep to the non-committal terms, hypopallium anterior and posterior.

The stria terminalis. Some confusion has arisen in the use of this term and of the term "olfactory projection tract." Johnston (1922) includes in the stria terminalis all fibres which run medially from the amygdaloid complex, dorsal to the fore-brain bundles. Since there is no general agreement about a more restricted use of the term, this seems the most satisfactory definition. Johnston gives a detailed analysis of these fibres in which the amygdalo-hypothalamic fibres or olfactory projection tract are included as "bundle 2." Crosby (1917) differentiates the stria terminalis from the olfactory projection tract, the former running between the pyriform cortex and nucleus of the lateral olfactory tract on the one hand, and the preoptic nucleus on the other; and the latter between the amygdala (her ventro-medial nucleus) and the hypothalamus. In this she has been followed by Herrick (1921). There does not seem to be any reason why so fundamental a distinction should be made between the preoptic and the hypothalamic connections of the amygdala, so that until more is known of the function and comparative anatomy of these tracts, it seems best to class them all as components of the stria terminalis. These can be described (following Johnston) according to their destination. On this basis the following components can be recognised in *Lacerta*:

(i) A hypothalamic bundle (Johnston's "bundle 2," the "olfactory projection tract" of S. Ramón y Cajal).

(ii) A large commissural bundle (Johnston's "bundle 1").

(iii) A small bundle running medially into the stria medullaris (Johnston's "bundle 5").

(iv) A small bundle to the preoptic region. This may be Johnston's infracommissural "bundle 3." It is not very clearly defined from the hypothalamic bundle in *Lacerta.*

These components were all described by Crosby for the alligator, the hypothalamic bundle from her ventro-medial nucleus and the others chiefly from the nucleus of the lateral olfactory tract. They were also described, with minor differences, by Johnston in the turtle, although he also found a bundle connecting the amygdala with the parolfactory area (paraterminal body) which seems to be lacking in *Lacerta.* Cairney describes preoptic and hypothalamic connections, but no commissural or habenular connections.

All these components of the stria terminalis arise in *Lacerta* from the central mass of the amygdaloid with the exception of some of the commissural fibres, which arise from the hypopallium posterior and run in the hypopallial component of the commissure. It follows that the central mass represents the nucleus of the lateral olfactory tract combined with Johnston's central and medial amygdaloid nuclei, or Cairney's and Durward's anterior amygdaloid nucleus, or Crosby's ventro-medial nucleus.

If the term "olfactory projection tract" is to be used at all, it would seem best to accept Crosby's definition of it, as including those fibres which connect the lateral olfactory centres of the hemisphere wall with the hypothalamus. Crosby differentiates a dorsal and ventral olfactory projection tract. The

former is clearly Johnston's "bundle 2" (cf. above). The latter is mentioned by Johnston, who suggests that it is homologous with the tractus pallii of Selachians. It is described and figured by Herrick for the frog, and clearly corresponds with the amygdalo-peroptic connection (fig. 13, *Amy. preop.*, and p. 173) of *Lacerta*.

The amygdaloid complex of *Lacerta* can be said to agree very closely in all its main characteristics with that of the other orders of Reptiles. It is chiefly remarkable for the great development and differentiation of the hypopallium posterior and the lack of differentiation in the remaining part, the central mass. Of the many outstanding problems in the morphology of this region, one of the most important concerns the development of the hypopallium posterior and its possible relation to cortical areas like the pyriform.

THE PARATERMINAL BODY

This region is well-developed in *Lacerta viridis* and can be defined in much the same terms as were used by Elliot Smith in 1901 to define the same region in Mammals. Its boundaries and the structures differentiated within it are shown in the reconstruction (fig. 20), and in the transverse sections (figs. 4–10).

It forms the whole thickness of the medial hemisphere wall between the ventral edge of the hippocampal cortex above the tuberculum olfactorium and palaeostriatum below. Posteriorly it extends to the lamina terminalis with the hippocampal and anterior commissures in it, and also above the hippocampal commissure and foramen of Monro to a point in the medial hemisphere wall just behind the posterior pallial commissure[1], or commissura aberrans of Elliot Smith (1903). Anteriorly it is bounded by the nucleus olfactorius anterior. The ventral boundary is the least definite, particularly just anterior to the lamina terminalis where the diagonal band fibres are entering (figs. 7, 8). Here it is practically indistinguishable from the posterior part of the palaeostriatum and the central amygdaloid mass.

Anteriorly the paraterminal body is characterised by the fewness of its cells (fig. 5). It does not bulge into the ventricle here, and shows no differentiation except the nucleus olfactorius medialis which has already been described (figs. 4, 20, *N. olf. med.*, and p. 167).

In its middle part (figs. 6–8) its most characteristic differentiation can be seen. It forms a marked prominence into the cavity of the lateral ventricle, and contains many more cells. These are arranged as a dorso-lateral nucleus of large irregularly pyramidal cells, rather loosely packed, and a ventro-medial nucleus of smaller rounder cells considerably more numerous than the dorso-lateral large cells. Very soon, going posteriorly, this differentiation becomes less clear (fig. 8), and the two nuclei, so far as they can be recognised at all,

[1] Since there is now no doubt that the "posterior pallial commissure" is a commissure of the posterior part of the hippocampal formation, "hippocampal" would be a more accurate term to apply to it than "pallial," and would avoid the vagueness associated with that word. The term "posterior hippocampal commissure" will be used throughout this paper.

become dorsal and ventral and are differentiable only by the size of cell. The ventral nucleus shows a tendency to divide into medial and lateral parts, but this apparent division is due to the fibres of the medial fore-brain bundle, which are passing through it here. The next definite differentiation can be called the nucleus of the diagonal band (figs. 8, 20). It extends up into the medial part of the paraterminal body from the region just in front of the preoptic recess, and back over the commissure among the fibres of the diagonal band as far as the level of the foramen of Monro. In fig. 9 the commissures appear, and the paraterminal body is seen dorsal to the hippocampal commissure and lateral to the descending fibres of the alveus system. It is this part of the paraterminal body which extends back to the posterior hippocampal commissure. It can be called the supraforaminal part because of its relation to the foramen of Monro. It contains the nuclei of the hippocampal and posterior hippocampal commissures (figs. 9, 10), but beyond this differentiation is indefinite. Medially and dorsally its cells are larger and are related to the alveus fibres. Ventro-laterally they are smaller. These two regions may represent the dorso-lateral and ventro-medial nuclei seen anterior to the lamina terminalis.

The nucleus of the hippocampal commissure is situated between the descending alveus fibres of both sides (figs. 9, 20). It lies dorsal to the commissure, and is closely related above to the diagonal band and its nucleus. The part of the nucleus in actual contact with the commissure consists of slightly smaller cells than the dorsal part.

The nucleus of the posterior hippocampal commissure (figs. 10, 20) consists of two parts, a medial, containing comparatively few cells of medium size, scattered among the fibres of the commissure itself, and a lateral, made up of small round cells, fairly tightly packed and lying immediately beneath the ependyma of the ventricle, and just above the membranous part of its medial wall.

The connections of the paraterminal body are numerous and difficult to unravel. Speaking generally, it may be said that it is connected dorsally with the hippocampal cortex, ventrally with the tuberculum olfactorium, diagonal band and medial fore-brain bundle, and anteriorly with the olfactory tracts, so that it lies in the path of most of the impulses passing to or from the hippocampus. In addition, it forms a bed in which the hippocampal and posterior hippocampal commissures lie. The large size of this body in Reptiles suggests that it is an important correlation centre.

Very few fibres enter the paraterminal body directly from the olfactory tracts in the olfactory peduncle. Most of them are relayed in the nucleus olfactorius anterior, the tuberculum olfactorium or the nucleus olfactorius medialis, although the latter may be regarded as a part of the paraterminal body. Fibres from the tuberculum olfactorium are particularly numerous (fig. 12, *F*). Most of these afferent olfactory fibres seem to go to the ventro-medial nucleus.

The diagonal band connects medial and lateral olfactory centres. It

begins in the lateral part of the central amygdaloid mass, sweeps ventrally behind the tuberculum olfactorium and ascends through its nucleus anterior and a little lateral to the preoptic recess (fig. 13). The fibres then turn back over the hippocampal commissure (fig. 19), probably making connection with its nucleus, and end by being distributed to the supraforaminal part of the paraterminal body and to the superficial aspect of the hippocampal cortex among the tangential fibres (figs. 13–15). The termination of some of the diagonal band fibres can be seen in fig. 18 (*D.B.*) just in front of the posterior hippocampal commissure. They are cut transversely in figs. 13–15, lying medial to the descending alveus fibres, through which they must penetrate to reach the paraterminal body.

The medial fore-brain bundle is the largest single tract connected with the paraterminal body. Its fibres enter in that region in front of the commissures where the dorso-lateral and ventro-medial nuclei are particularly well developed, and most of them run into the dorso-lateral nucleus (figs. 12–14, 18, 19). A few appear to be continuous with alveus fibres (fig. 13), a few enter the medial part of the paraterminal body, while others sweep back over the commissures to its supraforaminal part. These fibres lie lateral to the alveus fibres, while the diagonal band fibres, which have a similar distribution, lie medial (fig. 14). Those fibres of the medial fore-brain bundle which reach farthest anteriorly appear to end in the palaeostriatum. A few enter the anterior end of the paraterminal body, and appearances suggest that there is a connection between the palaeostriatum and the paraterminal body. This last point is not certain.

The medial fore-brain bundle carries impulses in both directions between the paraterminal body and the hypothalamus, mid-brain and possibly thalamus.

The largest dorsal connection of the paraterminal body is with the alveus system of fibres which arises on the ventricular surface of the hippocampal cortex. It extends beyond the lateral margin of the hippocampus underneath the dorsal cortex, but whether it carries fibres from the dorsal cortex as far as the paraterminal body and hippocampal commissures is not certain. Probably it does. Fibres which appear to belong to this system begin anteriorly where the hippocampus merges with the nucleus olfactorius anterior. They run caudally in the dorsal part of the paraterminal body (fig. 19), lying lateral to a superficial bundle from the tangential system which has a similar direction just under the pia (fig. 12). Some of these fibres probably end in the dorsal part of the paraterminal body, but most run back to enter the hippocampal commissure. The rest of the alveus system can be described in two parts, anterior and posterior to the posterior hippocampal commissure.

Most of the anterior fibres converge to the hippocampal commissure. Some run straight into the medial fore-brain bundle anterior to the anterior commissure, while others descend either through or behind the commissure to the hypothalamus (columns of fornix, fig. 14, *C.F.*) or into the stria medullaris as the medial cortico-habenular tract. As far as the paraterminal body is con-

cerned, there is no doubt that many alveus fibres connect with its dorso-lateral nucleus, although most are situated actually in the dorso-medial part of the body. Perhaps some fibres run into the ventro-medial nucleus, but this is not certain, for these medial fibres become very mixed with the fibres of the tangential system and it is not possible to differentiate them clearly.

The posterior part of the alveus system falls into three subdivisions:

(i) Fibres which arise from the ventricular surface of the hippocampus and run forwards above the posterior hippocampal commissure to connect with the paraterminal body (supraforaminal part) (fig. 17, *Alv.* (*i*)), but mostly to run into the hippocampal commissure. These fibres have no connection with the nucleus of the posterior hippocampal commissure.

(ii) Fibres which arise also from the ventricular surface of the hippocampal cortex, effect connections with the nucleus of the posterior hippocampal commissure and then run above the commissure, turn ventrally in front of it, and join the medial cortico-habenular component of the stria medullaris (fig. 17, *Alv.* (*ii*)).

(iii) Fibres which appear to arise from both surfaces of the hippocampal cortex, make connection with the nucleus of the posterior hippocampal commissure and then cross in the commissure (fig. 17, *Alv.* (*iii*)).

The alveus connections, so far as they concern the paraterminal body, can be summarised as follows. They connect the hippocampal cortex with the dorso-lateral nucleus and with the supraforaminal part of the paraterminal body. Some fibres run apparently without interruption through the paraterminal body into the medial fore-brain bundle, probably on their way to the hypothalamus. The rest are concentrated in the hippocampal commissure, where they effect connections with the nucleus of the commissure, or are connected to the nucleus of the posterior hippocampal commissure. From here they are relayed to the commissure itself or to the stria medullaris.

The tangential system of fibres superficial to the cortex is also connected to the paraterminal body. Anteriorly the system is continuous with the plexus of fibres superficial to the nucleus olfactorius anterior, which probably receives olfactory tract fibres. In this region it gives rise to the anterior olfacto-habenular tract (figs. 12–14) which runs ventrally over the anterior part of the paraterminal body and sweeps laterally under the tuberculum olfactorium. Other fibres from the tangential system enter the dorsal part of the paraterminal body and run ventro-posteriorly medial to the alveus fibres. They probably end in this part of the paraterminal body for they cannot be traced far, and soon become indistinguishably mixed with the alveus fibres; they may run as far ventrally as the ventro-medial nucleus. More posteriorly there is an obvious connection between the tangential system and the diagonal band fibres. It seems probable that these connections are efferent from the medial part of the paraterminal body and diagonal band to the superficial surface of the hippocampus.

It would be well at this point to recapitulate the connections of the nucleus

of the hippocampal commissure. It is connected to the central mass of amygdaloid by the diagonal band fibres, to the hippocampus by alveus fibres, and to the strio-amygdaloid complex by a few fibres which enter it from the anterior commissure. Posteriorly it may be connected to the medial cortico-habenular tract. This is probable, but not quite certain.

The position of the paraterminal body was defined at the beginning of this section. Its chief differentiations appear to be: a large-celled dorso-lateral and a small-celled ventro-medial nucleus, both best developed in its middle part; a nucleus of the diagonal band, and nuclei of the hippocampal and posterior hippocampal commissures, all consisting of small cells; and a nucleus of the medial olfactory tract which can only doubtfully be included in this region. There is also an anterior part containing comparatively few cells and showing no differentiation.

It receives olfactory fibres from the olfactory tracts anteriorly and from the diagonal band posteriorly. It is probable that these are transmitted on to the hippocampus by the tangential system. Some, and particularly those of the diagonal band, do not appear to get further than the paraterminal body itself, which, in these animals, is an important correlation centre. The alveus fibres carry impulses from the hippocampus and possibly the dorsal cortex as well, chiefly to the dorso-lateral part of the body, whence they appear to be relayed to the hypothalamus *via* the medial fore-brain bundle. Whether this bundle carries ascending impulses as well must at present be left an open question; it seems probable that it does, but there is no evidence in this material to decide the point. The most important connections of the nuclei of the commissures, apart from their connections with the commissural fibres themselves, appear to be with the habenular ganglion *via* the medial cortico-habenular tract. The significance of the possible striatal and amygdaloid connections of the nucleus of the hippocampal commissures is obscure. It is disappointing that more definite differences in the connections of the dorso-lateral and ventro-medial nuclei of the body cannot be made out from the fibre-stained series, for the differentiation in cell-stained series is very distinct.

Discussion

A survey of the literature shows a very large measure of agreement concerning the cell masses and fibre connections of the paraterminal body, but once more the agreement is obscured by the varieties of terminology which have been used.

The name "paraterminal body" was introduced by Elliot Smith (1901). He defined it, and pointed out that the structures included in it form an essential unity in that they all serve as relay stations in the course of fibres going to or coming from the hippocampal cortex. The name "paraterminal body" implies no doubtful homologies and is topographically appropriate. It has the additional advantage that it was from the first precisely defined, and that the same definition is applicable to this region, with minor variations, in all the vertebrate

classes. The other two terms commonly used, "septum" and "parolfactory area," are unsatisfactory, because the first implies human homologies which cannot be substantiated, and the second has no precise definition and has been used in different senses by different writers (p. 168). Against this it may of course be urged that the word "septum" has the advantage of brevity, that it has become generally accepted by European and American workers, and that the misconceptions underlying its first use have been forgotten and no longer deceive anyone. It is also a convenient word from which compound terms, e.g. "tractus septo-corticalis," can be built.

The cellular differentiation of the paraterminal body has been investigated chiefly by Americans. Medial and lateral nuclei have been very generally recognised (e.g. Herrick, 1910). Johnston (1913) distinguished the upper part as "primordium hippocampi" and Herrick (1910) included in the lower part the "nucleus accumbens," grouping all these structures in the ventro-medial section of the hemisphere wall. It is now generally agreed that the nucleus accumbens should be excluded from the paraterminal body (septum) and placed with the palaeostriatum (Cairney, 1926; Durward, 1930; Kappers, 1921; Johnston, 1922). No further discussion of this point is necessary.

The term "primordium hippocampi" was introduced by Elliot Smith (1903) and applied by him to that area of the brain of Fishes and Amphibia which is homologous with the hippocampal formation of Reptiles and Mammals, but does not show the histological characteristics which are distinctive of the higher groups. He distinguished this primordium hippocampi from the part of the paraterminal body which extends back above the hippocampus in the frog. Herrick appears to have used the term in the same way for Amphibia in 1910, and again in the figures of his later paper (1921) which is not primarily concerned with this particular region.

Confusion has arisen in the description of Reptiles. Many Reptiles show a well-developed posterior extension of the paraterminal body above the commissures and the foramen of Monro, the supraforaminal part. Johnston calls the dorsal part of the paraterminal body, including the supraforaminal part, "primordium hippocampi." His chief reason for this is embryological. He locates the point of closure of the neuroporic recess between the anterior and hippocampal commissures, and states that all the hemisphere wall above this point is "pallial" and all below "basal." This appears to be a purely arbitrary division, for there seems no reason why the point of closure of the neuropore should be a morphological boundary between these regions. Assuming, however, that it is, it does not follow that any part of the brain wall above it must be hippocampus, or primordium hippocampi, unless it can be shown that it does in some Vertebrate develop into a definitive hippocampal formation. There is no reason why a "pallial" part of the brain wall should not contribute to the adult paraterminal body just as it appears to contribute to the corpus striatum on the lateral side. Now there is no evidence that the supraforaminal part of the paraterminal body of Reptiles ever does differentiate into a true

hippocampal cortex, so that the justification for calling it a "primordium hippocampi," as Johnston does, seems very slight indeed. All one can say is that it develops in a part of the brain wall above the level of the neuroporic recess. Whether it should therefore be called "pallial" must remain a matter of opinion, and will depend upon the reliance one is inclined to place on the position of the neuroporic recess as a fundamental morphological landmark in the brain. The question still remains whether, in the adult, there is any other reason for separating the dorsal part of the paraterminal body and for giving it a distinct name. Its chief characteristic is that it contains a large number of alveus fibres crowded together and mixed with fibres from the tangential system superficial to the hippocampus. On this account it has been called the "pars fimbrialis septi" by Kappers. There can be no morphological objection to this term, for it includes the part in question in the paraterminal body or septum, but it seems a little unnecessary to have a separate name for a region which is distinguished only by a crowding together of fibres in it. Both Cairney and Durward found it convenient to describe the paraterminal body of *Sphenodon* without the separation of a part corresponding to Johnston's primordium hippocampi. Their description agrees very closely with the condition in *Lacerta*. Shanklin (1930), in the chameleon, describes similar findings. Neither Herrick's figures (1910) nor Johnston's (1915) for the turtle, nor Crosby's (1917) for the alligator, in which the primordium hippocampi is indicated, show it as a clearly differentiated region in the adult. They give rather the impression that the condition in both turtle and alligator may be essentially similar to that in *Lacerta* and *Sphenodon*, and that the similarity has been obscured by the terminology used. It is impossible to say more without a first-hand knowledge of the animals in question, but the evidence suggests that the description of the paraterminal body or septum in Reptiles would be considerably simplified by the dropping of this term "primordium hippocampi," at least until more substantial evidence either from embryology or adult anatomy can be adduced in its favour.

The relationship between the anterior commissure and the paraterminal body has already been discussed (p. 176). Since the anterior commissure contains only a few fibres which run to or from the hippocampus, it seems reasonable that the cells which surround it should be excluded from the paraterminal body, and this is what the material suggests.

Obviously many of the suggestions which have been made concerning the interpretation and terminology of the paraterminal body are provisional, but the evidence as it stands justifies a preliminary statement of the general cellular structure of the reptilian paraterminal body in the following terms.

The definition given by Elliot Smith in 1901 is applicable to the reptilian paraterminal body, but with the exclusion of the bed of the anterior commissure. It contains medial and lateral nuclei (ventro-medial and dorso-lateral in *Lacerta*) which are respectively afferent to and efferent from the hippocampus. It contains the bed and nucleus of the hippocampal commissure and of the

posterior hippocampal commissure when present, and the nucleus of the diagonal band.

The fibre connections do not vary much in the different forms described, but certain variations in terminology may be mentioned. The diagonal band was seen and figured by Unger in the gecko and by de Lange in *Varanus*, and given the name "tractus cortico-parolfactorius," its connection with the amygdala being overlooked. Various workers, chiefly in the European schools, have used such terms as "tractus cortico-septalis," "tractus cortico-olfactorius septi," etc., for tracts connecting the cortex, paraterminal body and tuberculum. Sometimes "parolfactory" is substituted for "septal" in these compound terms, but all of them, provided Edinger's use of the term "parolfactory area" to include the medial part of the tuberculum and the grey matter beneath it is remembered, are self-explanatory and unlikely to lead to confusion. Johnston describes a connection between the amygdala and the paraterminal body *via* the stria terminalis in the turtle. Whether this connection is generally present in other forms or not cannot be decided from the literature, and it seems a point worthy of more attention. I cannot find definite evidence of it in *Lacerta*. The habenular connections *via* the stria medullaris also do not appear to have been completely unravelled. In the literature they are represented by "septo-habenular" fibres (Herrick, 1910; Cairney, 1926), while the medial cortico-habenular fibres are probably relayed to some extent in the nuclei of the hippocampal or posterior hippocampal commissures. I do not find definite evidence in *Lacerta* for habenular connections with the paraterminal body except for the connections to the nuclei of the commissures. The "anterior olfacto-habenular" tract was described by Herrick (1921) in the frog, and by Meyer, de Lange, and Cairney, in different reptilian orders. Herrick (frog) and de Lange (*Varanus*) describe it as connected with the paraterminal body, Cairney (*Sphenodon*) with the tuberculum olfactorium. In *Lacerta* it appears to run up to the anterior end of the hippocampal formation or nucleus olfactorius anterior. It seems probable that the fibres running from the paraterminal body to the habenular ganglion all carry impulses relayed from the hippocampus. Most of them come from the nuclei of the hippocampal and posterior hippocampal commissures. A few may come from other parts of the paraterminal body (Herrick, Cairney) but it is not yet possible to say precisely what part. Most of them run medially direct to the habenula, but a few from the anterior end of the paraterminal body may run laterally under the forebrain bundles to join the stria medullaris from the lateral side. With the latter may be some fibres from the nucleus of the diagonal band.

THE PALLIUM

The pallial area of the lacertilian hemisphere is situated dorsally, dorsomedially, and laterally. It stretches from the nucleus olfactorius anterior back to the posterior pole of the hemisphere. The nucleus olfactorius anterior is particularly closely related to the three main divisions of the pallium since

where it is traced posteriorly it is found to blend with each of them. These areas (e.g. fig. 5) are: dorso-medially, the hippocampal cortex; laterally, the pyriform cortex; and in between the two an area, which can be called the "dorsal cortex." All these areas blend posteriorly in an undifferentiated cap of cortex over the posterior pole of the hemisphere.

The pyriform cortex

This begins anteriorly in the dorso-lateral region of the nucleus olfactorius anterior (fig. 3, *D*), where there is an accumulation of cells among which the fibres of the lateral olfactory tract are scattered. Soon it becomes separate (fig. 4), and the lateral olfactory tract takes up its position close to the endorhinal fissure between it and the tuberculum olfactorium. Dorsally it overlaps the dorsal cortex (fig. 4). Figs. 5 and 6 show the typical appearance in the anterior part of the hemisphere: a fairly clearly defined cell layer, superficial to the dorsal cortex above, and continuous with the hypopallium anterior below. This continuity is not clear in every section, but is sufficiently marked at least to suggest an inrolling of the ventral edge of the pyriform to form the hypopallium anterior. Posteriorly (figs. 7, 8), this appearance is lost, and the whole pyriform cortex is smaller. At the posterior end of the hemisphere (fig. 10) it loses its individuality, forms a continuous layer with the dorsal cortex above, and joins the hypopallium posterior below.

Throughout its extent the pyriform cortex shows a rather indefinite division into dorsal and ventral parts, the former consisting of larger cells than the latter (fig. 9).

The hippocampal cortex

The first break to occur in the undifferentiated cortical ring of the nucleus olfactorius anterior is that between the pyriform and the dorsal cortex. Next, just posterior to it, a break appears medially (fig. 4) in the region of the anterior end of the paraterminal body. A cap of cells is now to be seen over the dorsal wall of the ventricle, tucking under the pyriform laterally to come into continuity with the anterior end of the hypopallium, and extending medially into the dorsal part of the medial hemisphere wall above the paraterminal body. It consists at first of rather diffusely arranged cells of irregular shape and medium size. Very soon the medial part of this region takes on the appearance typical of the hippocampal cortex in the posterior parts of the hemisphere. It becomes compact, very sharply defined from the white matter on either side of it and the paraterminal body ventral to it. It extends just on to the dorsal surface of the hemisphere round the dorso-medial angle and passes at first without any break into the dorsal cortex. Soon a kink appears, so that at the point of transition the hippocampus comes to overlap the dorsal cortex slightly. Just behind this level it breaks off from the dorsal cortex (fig. 5). It now consists of medial and lateral parts. The medial part is made up of small pyramidal cells, closely packed into a very clearly defined plate, and the lateral

of a thin tail of cells, pyramidal in shape but much larger and less regularly arranged than the cells of the medial part. These parts will be called the small- and large-celled parts of the hippocampal cortex respectively (fig. 6, *Cx. hip. s. c.* and *Cx. hip. l. c.*). The large-celled part is at first fairly thick (3 or 4 cells) and of short extent medio-laterally. It becomes progressively more extensive, and thinner (1 or 2 cells thick). Behind the posterior hippocampal commissure it extends as far as the lateral aspect of the hemisphere. It remains distinct from the dorsal cortex until just in front of the posterior pole of the hemisphere, where it blends with it. The small-celled medial part of the hippocampus also increases in extent from before backwards, so that the greater part of the cap of cells over the posterior pole is formed by it. It bulges slightly into the cavity of the lateral ventricle on its medial wall, except at the anterior and posterior ends.

There are two sulci related to the hippocampal cortex. One, on the medial hemisphere wall, the fissura limitans hippocampi, has already been discussed (p. 159). The other, a ventricular sulcus, is situated just above the level of the ventral edge of the hippocampus and lies between the paraterminal body and the alveus system of fibres (figs. 6–9). It seems to be caused by the bulging of the paraterminal body into the ventricle and is not well marked till a definite dorso-lateral nucleus has developed. It becomes shallower behind the level of the hippocampal commissure, and has disappeared before the posterior hippocampal commissure is reached. This is Johnston's "fimbrio-dentate sulcus," but he applies this same name to the fissura limitans hippocampi.

The dorsal cortex

The origin of the dorsal cortex anteriorly in the nucleus olfactorius anterior has already been described. It soon becomes broken off from the pyriform cortex and is then for about ½ mm. or less continuous laterally under the pyriform cortex with the hypopallium anterior (fig. 4). The hemisphere wall is naturally thick in this region, since both pyriform and dorsal cortex lie between the pia and the ventricle, but no ventricular ridge is produced as described by Elliot Smith and Johnston in the turtle. At first continuous medially with the hippocampus, the dorsal cortex soon separates and is then overlapped medially by the large-celled part of the hippocampus as it is laterally by the pyriform (fig. 5). These relationships are preserved back to the posterior pole of the hemisphere, where the dorsal cortex becomes continuous with the pyriform laterally and the hippocampus medially, and loses its individuality.

The cells of the dorsal cortex begin anteriorly by being fairly large and rounded, resembling those of the hypopallium with which it is continuous. As it breaks away from the hippocampus its medial part is seen to be made up of slightly smaller, irregularly pyramidal cells (resembling those of the large-celled hippocampus, but smaller), and gradually the whole dorsal cortex takes on a similar cell type. The medial part, however, rather more than just the area

overlapped by the hippocampus, is differentiated from the lateral almost to the posterior pole of the hemisphere by the slightly looser and more irregular arrangement of its cells, and by its greater thickness. The dorsal cortex can be described then as a rather irregular and not very well-defined cortical sheet, in which there is a tendency for a medial strip to differentiate from the rest. It is continuous anteriorly with the nucleus olfactorius anterior and the hypopallium anterior and is overlapped medially and laterally by the hippocampal and pyriform cortex respectively.

The fibre connections of the pallial areas can be classified as follows.

The tangential system. This is common to all three pallial areas, and consists of a network of fibres lying superficial to them. Anteriorly it is continuous with a similar network over the nucleus olfactorius anterior, which probably receives olfactory tract fibres. It is best developed over the hippocampal cortex. Here it receives olfactory tract fibres anteriorly and gives rise to a small but compact bundle, the anterior olfacto-habenular tract. Behind this level the tangential fibres are connected with the upper part of the paraterminal body and with the fibres of the diagonal band (figs. 12–15). Behind the posterior hippocampal commissure there are many bundles of fibres which pierce through the hippocampal cortex joining the tangential system to the alveus system. Laterally, on the pyriform, the tangential system is not well developed, although it is fairly conspicuous anteriorly. Here it may also receive olfactory tract fibres, and probably sends fibres from the pyriform cortex into the diagonal band and the stria medullaris to the lateral part of the amygdaloid mass (fig. 13), and possibly to the amygdaloid component of the anterior commissure. Over the dorsal cortex the tangential system is less compact. No definite connections can be found for it, except possibly with olfactory tract fibres anteriorly. It probably consists of association fibres between the dorsal, hippocampal and pyriform cortex.

The alveus system. These fibres lie just outside the ependyma of the ventricle beneath the hippocampal formation, and it can at once be said of them that the majority from the anterior two-thirds of the hemisphere converge to the hippocampal commissure, and from the posterior third to the posterior hippocampal commissure. The fibres which enter the hippocampal commissure mostly join the hippocampal formations of the two sides. Some appear to pass into the amygdaloid component of the anterior commissure (fig. 14) to join the central amygdaloid mass of the opposite side. The posterior hippocampal commissure not only links the posterior third of the hippocampus of one side to that of the other, but also conducts fibres from the hippocampus to the medial cortico-habenular tract of the opposite side. There are many additional connections. Anteriorly alveus fibres enter the upper part of the paraterminal body (fig. 12). Their course and destination have already been described (p. 184). It is enough to say here that they connect with the dorso-lateral nucleus of the paraterminal body itself, with the hypothalamus through the medial fore-brain bundle and the columns of the fornix, with the nuclei of both

hippocampal and posterior hippocampal commissures, and with the habenular ganglia through the medial cortico-habenular tract. It is noteworthy that fibres descending to the hypothalamus pass both anterior to, through, and posterior to the anterior commissure. In fig. 14 the most lateral of these descending fibres (*C.F.*) run into the medial cortico-habenular tract.

In view of the doubt over the homologies of the dorsal cortex, the extent of its connection with the alveus system is important. At the extreme anterior end of the hemisphere, where the hippocampal and dorsal cortex are not clearly differentiated, the alveus system extends laterally under what is continuous posteriorly with the dorsal cortex. Behind this level the alveus is connected with the medial part of the dorsal cortex and, at the level of the hippocampal commissure, this connection extends laterally until it includes all the dorsal cortex except its extreme lateral edge. Whether these fibres actually have similar connections to those described above for the alveus system, or whether they are only associational between the dorsal cortex and the hippocampus, it is impossible to say with complete certainty. The appearances are strongly in favour of the first of these alternatives. This connection of the medial part of the dorsal cortex with the alveus seems to correspond with the cellular differentiation described above.

The remaining pallial connections concern the dorsal and the pyriform cortex. Anteriorly where the dorsal cortex turns in beneath the pyriform to join the hypopallium anterior several fasciculi leave it and run ventro-caudally to join the olfactory component of the anterior commissure (fig. 17). The same region receives a few fasciculi from the lateral fore-brain bundle. Posterior to this region fasciculi can be seen collecting on the ventricular surface of the lateral part of the dorsal cortex (fig. 12), in the same plane as the medially placed alveus fibres. They run ventrally and posteriorly to join the hypopallial component of the anterior commissure (fig. 14).

Finally, there is the connection of the lateral olfactory tract with the pyriform cortex. Anteriorly the deep surface of the pyriform gives fibres to and receives them from the lateral olfactory tract, and it is possible that a further interchange occurs along the ventral edge of the pyriform before the lateral olfactory tract has entered the amygdaloid region.

The cortical fibre connections can be summarised as follows. All three cortical areas are connected by association fibres which probably run in the tangential system. Medially the hippocampus receives olfactory tract fibres anteriorly, diagonal band fibres from the central amygdaloid mass and possibly pyriform cortex, fibres from the paraterminal body (probably the ventro-medial nucleus), the tuberculum olfactorium, and the medial fore-brain bundle. Many of these fibres enter the tangential system and they are probably mostly afferent. Its main efferent tract is the alveus, which connects it with the hippocampus and the amygdaloid complex of the opposite side, with the paraterminal body (dorso-lateral nucleus), with the hypothalamus *via* the columns of the fornix and the medial fore-brain bundle, and with the habenular

ganglion of the same and the opposite sides. The dorsal cortex is connected in its medial part anteriorly, and posteriorly for almost its whole medio-lateral extent, with the alveus system. Laterally and anteriorly it gives commissural fibres to both olfactory and hypopallial components of the anterior commissure, and is connected with the lateral fore-brain bundle. The pyriform cortex receives fibres from and gives them to the lateral olfactory tract, and probably gives fibres to the amygdaloid complex (lateral part), to the diagonal band, and to the stria medullaris (habenula). It may provide some fibres for the amygdaloid component of the anterior commissure.

Discussion

It is clear that the division of the cortex into the three areas to which the terms "hippocampal," "dorsal," and "pyriform" have been applied, is a very uniform condition throughout the reptilian class. There is some variation in the degree to which the areas are differentiated from one another. In *Sphenodon* they are practically continuous, although there is a tendency for the dorsal edge of the pyriform to overlap the dorsal cortex (Durward, 1930). The continuity is rather more marked in the alligator (Crosby). In the turtle the pyriform is distinct from the dorsal cortex, while in Lacertilia all three areas are discontinuous for the greater part of their extent. In Ophidia the pyriform does not appear to be so clearly differentiated from the dorsal cortex, but otherwise the condition is similar to the Lacertilia (Edinger, Meyer). It is characteristic that when the dorsal cortex is a differentiated area, it tends to be overlapped by the hippocampus medially and the pyriform laterally (the medial and lateral superposition of de Lange). It is also characteristic that when the lateral edge of the hippocampus is separate from the dorsal cortex, it consists of a tail of large pyramidal cells, rather irregularly arranged, which can be called the "large-celled" to contrast with the "small-celled" part of the hippocampus (cf. Unger).

An anterior thickening of the dorsal cortex, where it bends round laterally to come into contact with the anterior end of the hypopallium anterior, has been described in most orders. This thickening sometimes produces a ridge projecting into the lateral ventricle, e.g. in the turtle (Elliot Smith, Johnston), and is connected to the thalamus by fibres of the lateral fore-brain bundle.

The only cortical area which shows a uniform and characteristic type of differentiation is the medial (small-celled) part of the hippocampus. The other areas usually consist of a single more or less well-defined layer of cells. Unger, for the gecko, has described a distinct double layer in the dorsal cortex.

So far as they have been described here, the fibre connections of the cortical areas in *Lacerta* agree for the most part with those described in other forms. There are differences in detail, particularly concerning the cortico-habenular connections, but these are not more than one would expect to find, and probably have no great morphological importance.

The connections of the dorsal cortex have naturally claimed a great deal of

attention. There seems now very little doubt that at least its medial part sends fibres into the alveus system (S. Ramón y Cajal, Crosby, Unger, etc.), but the ultimate fate of these fibres deserves further investigation. Anteriorly and laterally the connection between the dorsal cortex and the thalamus *via* the lateral fore-brain bundle has been noted in all the types described. The fibres which run from the lateral part of the dorsal cortex into the anterior commissure, which are very definite in *Lacerta*, are not mentioned in the literature, although a remark by Kappers (1929, p. 141) implies a knowledge of them. In 1921 (p. 1033) he denied their presence.

The interpretations of these facts show many variations, most of which centre round the dorsal cortex. Kappers includes the dorsal cortex with the hippocampus in his "archi-cortex," saying that the small-celled hippocampus is fascia dentata, the large-celled, intermediate, and the dorsal cortex, cortex ammonis. Johnston maintains that the dorsal cortex is neopallial and that fibres from it which run to the hippocampal commissure are callosal fibres. Elliot Smith compromises between these two extremes by calling the dorsal cortex "parahippocampal" and comparing it with the subicular region of Mammals. He finds the homologue of the mammalian neopallium in the antero-lateral thickening of the dorsal cortex, his "primordium neopallii."

As has been stated more than once, our knowledge of the fibre connections of these cortical areas is not detailed enough to make it possible to decide certainly between these different interpretations. Kappers appears to depend for his justification chiefly on the similarity between the "medial superposition" of Reptiles (the overlapping of the dorsal cortex by the large-celled hippocampus) and the relationship between the fascia dentata and cortex ammonis of Mammals. He states further that the hippocampus (medio-dorsal cortex, or small-celled hippocampus) is receptive, and the dorsal cortex efferent to the alveus. In a general way this is perhaps true, but the appearances suggest strongly that many, if not most, of the efferent alveus fibres have their origin in the small-celled hippocampus, and certainly a considerable part of the dorsal cortex in *Lacerta* has its commissural fibres in the anterior commissure. Much more definite evidence than these general resemblances is needed to support a definite homology.

The view that the whole dorsal cortex is neopallial seems also to lack support. The neopallium of Mammals is a correlating mechanism of a high order, receiving ascending sensory impulses from the thalamus and giving descending motor impulses to the brain stem and lower spinal centres. When it first appears in monotremes its commissural fibres run in the anterior commissure. Only a comparatively small part of the dorsal cortex of Reptiles possesses these characteristics. This part is the anterior part of its lateral border, Elliot Smith's "primordium neopallii" and Johnston's "pallial thickening."

Fibres from the thalamus *via* the lateral fore-brain bundle to the dorsal cortex are definite, although in *Lacerta* they are scanty. Whether descending

motor fibres are present as well is still very doubtful, although Crosby has produced some histological evidence in their favour from Golgi preparations of the alligator brain. Johnston's experimental evidence (1916 *a*) is suggestive, but needs extension and confirmation. By the courtesy of Prof. Elliot Smith I have been able to see the unpublished description of an extensive series of experiments performed by Dr W. H. Wilson on the brain of *Varanus* and *Uromastyx*. These experiments were done primarily to investigate the electrical excitability of the optic lobes, but in every one the cortex of the hemispheres was stimulated. It was found that there was never a motor response from stimulation of the hemisphere by means of a current which was effective in producing a response from the mid-brain. This suggests that Johnston's results may have been due to a diffusion of the stimulus to neighbouring parts of the brain. Wilson's series included at least forty separate experiments.

That the commissural fibres of the lateral part of the dorsal cortex run in the anterior commissure is certain in *Lacerta*. It would be interesting to know whether this occurs in other Reptiles as well. That part of the dorsal cortex which receives these commissural fibres, or gives rise to them, corresponds very closely with Johnston's electrically excitable area (1916 *a*), and is more extensive than Elliot Smith's primordium neopallii (1919), that is, than the area receiving thalamic fibres. It diminishes in medio-lateral extent from before backwards, while in the same direction the area served by the alveus system increases. This suggests that the anterior and lateral part of the dorsal cortex is neopallial, with commissural fibres in the anterior commissure and the posterior and medial part "parahippocampal" with commissural fibres in the hippocampal commissure.

The presence or absence of callosal fibres in Reptiles will clearly depend upon the extent of the alveus system. If fibres enter it from the neopallial part of the dorsal cortex, and can be traced into the hippocampal commissure, they constitute the rudiments of a corpus callosum. In *Lacerta* the greatest area of dorsal cortex which could be called neopallial, using the criteria enumerated above, is that area served by fibres of the anterior commissure. Alveus fibres do not appear to extend into it, so that the evidence seems to be against the presence of callosal fibres, at least in *Lacerta*. At the same time it is impossible to make a rigid separation of the dorsal cortex into parahippocampal and neopallial parts, so that the question is bound to remain to some extent an open one.

The probable course of events in the evolution of the dorsal cortex can be stated provisionally in the following way. At first there is an area, comparatively undifferentiated, intermediate between the hippocampus and the pyriform cortex, and probably dominated by olfactory impulses from both of them. It may have discharged entirely through the alveus system, although the connection laterally with the anterior commissure may be equally primitive and indicate a relationship with the pyriform, just as the alveus connections indicate a relationship with the hippocampus. The intrusion of somatic

impulses from the thalamus into its lateral part is the first step in the development of a cortex primarily concerned with the correlation of non-olfactory impulses, i.e. the first step in the development of a neopallium. This step has been taken by the Reptiles. Whether in addition they have developed descending motor fibres is still doubtful. It is quite possible that in some Reptiles alveus fibres do extend laterally into this area connected with the thalamus, but a clear demonstration of them is so far lacking. If present it would be reasonable to describe them as callosal, since by their increase in the eutherian Mammals a definite corpus callosum would be differentiated from the hippocampal commissure. The medial part of the dorsal cortex which has retained its connection with the alveus system without acquiring thalamic connections seems, as Elliot Smith has suggested, to be comparable with the subicular cortex of Mammals. The latter is a narrow strip of cortex between the hippocampal and neopallial areas. It shows the typical histological structure of neither, but appears to send efferent fibres into the alveus system (the fornix longus, Kölliker, 1889, p. 780).

The views set out here correspond very closely with those of Crosby (1917) and Cairney (1926).

LARGE FIBRE TRACTS

So far all the different parts of the hemisphere have been described together with their fibre connections. It will make the structure of the brain clearer if certain large fibre tracts, the different components of which have already been mentioned separately, are now briefly described in their entirety.

The anterior commissure

The anterior commissure lies in the lamina terminalis, ventral and slightly anterior to the hippocampal commissure (fig. 20). Anteriorly it is related to the nucleus of the diagonal band, to the diagonal band fibres, and to fibres of the medial fore-brain bundle which run up in front of it (fig. 18). Ventral to it is the preoptic recess and preoptic nucleus. Posteriorly, and close to the medial plane is a comparatively cell-free region which separates it from the anterior end of the thalamus, while more laterally descending fibres of the alveus system (fig. 14, *C.F.*) and the tractus cortico-habenularis medialis (fig. 18) are found. Its bed is formed by a part of the brain which should probably be classed with the strio-amygdaloid complex rather than the paraterminal body. It contains no nucleus of the anterior commissure.

The commissure contains two chief components, which from the origin or destination of most of the fibres composing them, can be named hypopallial and amygdaloid components respectively (figs. 14 and 18, *Com. ant. hyp.*; *Com. ant. amy.*).

The amygdaloid component (figs. 14, 17, 18) lies in the anterior and ventral part of the commissure and collects fibres from the whole of the central amygdaloid mass and possibly the ventral edge of the pyriform cortex. It is

joined anteriorly by a compact fasciculus which can be called an olfactory component (figs. 12, 13, 17). It appears at the extreme anterior end of the hemisphere where it collects fibres from the dorsal cortex where it is rolled in under the pyriform cortex to come into contact with the hypopallium, and from the olfactory tracts, either directly or after a relay in the nucleus olfactorius anterior. It runs back among the fibres of the fore-brain bundles between the palaeostriatum and tuberculum, so that it may receive fibres from either of these structures, although this is not certain. It crosses in the upper and anterior part of the amygdaloid component. Most of its fibres come from the dorsal cortex in the region of the "primordium neopallii."

After crossing, some fibres leave the dorsal surface of the amygdaloid component to enter the alveus of the opposite side. These may contain the olfactory component. The rest connect either with the opposite amygdaloid, or the opposite hypopallium. Probably most of them go to the hypopallium.

The hypopallial component lies dorsally and posteriorly in the commissure. It contains fibres from: (i) the dorsal cortex; (ii) the hypopallium anterior; (iii) the hypopallium posterior; and (iv) parts of the central amygdaloid mass.

(i) This contribution consists of several fasciculi which collect from the lateral part of the dorsal cortex anterior to the level of the commissures (figs. 12–14). They run posteriorly, medially and ventrally to cross in the commissure.

(ii) Comparatively few diffusely arranged fibres which collect in the core of the hypopallium anterior at about the level of the commissures (fig. 14). The anterior part of the hypopallium anterior has no commissural fibres, or very few. Behind the commissures these fibres are joined by many fairly large fasciculi which arise from the posterior part of the hypopallium anterior, but from its ventricular surface.

(iii) A large number of fibres which arise from the ventricular surface of the hypopallium posterior. They are seen running anteriorly in fig. 16 (*Com. ant. hyp.*).

(iv) A few fibres which join (iii) from the ventral part of the central amygdaloid mass (fig. 16, *E*).

Many of the fibres of the hypopallial component of the commissure run between the same regions of opposite sides. Some appear to cross obliquely and to run to the central amygdaloid mass on the opposite side (fig. 14). No connection was apparent between this component and the alveus system. Naturally the fate of any of the fibres which enter the anterior commissure is very difficult to determine, as they are all mixed in a compact bundle as they cross the medial plane.

Components corresponding approximately to the hypopallial, amygdaloid and olfactory components of *Lacerta* (the latter joining the amygdaloid component) have been described under various names throughout the literature.

The hypopallial component has usually been named the "pars epistriatica," or "inter-epistriatica" (de Lange, Edinger, Kappers, etc.). In the alligator it

appears to be small and to join the amygdaloid component (Crosby's "stria terminalis component"). It is well developed in a snake (*Callopeltis aesculapii*, Meyer, 1893, "markloses Theil der Commissura anterior") and has been described in other Lacertilia (de Lange, 1911; Shanklin, 1930, etc.). In the alligator it appears to consist of only a few fibres from the extreme ventro-lateral part of the dorso-lateral area (hypopallium) (Crosby, 1917).

The amygdaloid component corresponds undoubtedly with the "stria terminalis component" of American writers. This is described by Crosby as being connected to the pyriform cortex and the nucleus of the lateral olfactory tract, and by Johnston (1922) as essentially a commissure of the nucleus of the lateral olfactory tract. Shanklin (1930), in the chameleon, finds the same as Crosby in the alligator. In *Lacerta* its chief connection is with the central mass of the amygdaloid complex. It is probable that this central mass includes the greater part of the nucleus of the lateral olfactory tract which is a much more clearly differentiated structure in other forms.

A different terminology is used by the European writers, e.g. Edinger, Kappers, de Lange, Unger, etc. They distinguish a component of the commissure by the terms "pars corticalis" (Edinger), "tractus cortico-olfactorius cruciatus" (Kappers), or similar terms, all of which stress the connection of this component with the lateral (pyriform) cortex. This is almost certainly the same as my amygdaloid component and the stria terminalis component of the Americans. My findings are to some extent at variance with those of both European and American schools, in that the pyriform connections of this component are certainly few and possibly absent in *Lacerta*, while the amygdaloid connections (to the central mass) are conspicuous. It is possible that poor silver impregnation may account for this.

It should be noted that although the nucleus of the lateral olfactory tract is included in the central mass, the latter must represent other parts of the amygdaloid complex as well because of its connection with other components of the stria terminalis.

The olfactory component of *Lacerta* is apparently like that of other forms, except for its strong connection to the anterior and lateral part of the dorsal cortex (primordium neopallii). It is usually described as receiving fibres from the intermediate olfactory tract (Crosby), from the tuberculum olfactorium (Kappers' "anterior basal olfactory centres"), and from the nucleus olfactorius anterior (Edinger's "lobus olfactorius"). Unger (in the gecko) describes many of its fibres as running up to the hippocampal cortex after crossing in the commissure. In all these respects *Lacerta viridis* is probably like other Reptiles, although it is difficult to get completely convincing evidence in every case.

Kappers (1921) describes a bundle of fibres, the "radiatio frontalis commissurae anterioris." These, he says, arise in the septum (paraterminal body) and run ventro-posteriorly to cross anterior to the commissura pallii anterior (hippocampal commissure). His fig. 532, p. 1030, a sagittal section through the brain of *Varanus*, in which these fibres are shown, is very like my fig. 19. The

fibres he labels "rad. front." clearly correspond with my alveus fibres, sweeping back from the anterior end of the hippocampus to join the hippocampal commissure. Until there is clearer evidence available to show that there are fibres in this portion which come from the paraterminal body and do not belong to the alveus system, the question of the presence of such a component in the anterior commissure must be left an open one.

It is clear that there are a great many details in which our knowledge of the connections of the anterior commissure is incomplete. A careful investigation of the condition in Chelonia and in *Sphenodon* might be illuminating. Experimental lesions, with a study of the resulting degenerations, might be useful too, particularly for sorting out the connections of the olfactory component and for tracing fibres from one side of the brain to the other.

Stria medullaris

Under this term are included those fibres which connect various parts of the telencephalon with the habenular ganglia (epithalamus). It can be divided into medial and lateral parts which will be called for convenience "stria medullaris medialis" and "lateralis".

The fibres which run into the stria medullaris lateralis are collected from many different parts of the hemisphere and, following the common usage, can be described according to their origin in the following terms.

Lateral cortico-habenular fibres. These arise from the lower edge of the pyriform cortex and the outer part of the central amygdaloid mass (a part probably corresponding to the nucleus of the lateral olfactory tract), at about the level of the commissures. They can be seen running down beneath the pia mater to join the tractus olfacto-habenularis anterior in fig. 14.

Lateral olfacto-habenular fibres. These have a more widespread origin. Posteriorly they arise from the preoptic nucleus and perhaps the supra-optic nucleus. They can be seen in fig. 14 running laterally between the fore-brain bundles and the optic tract. Anteriorly they arise as a compact bundle of fibres, the anterior olfacto-habenular tract (Herrick, 1921) (figs. 12–14, *Tr. olf. hab. ant.*). In fig. 13 it crosses superficial to the diagonal band fibres, and is to some extent mingled with them (see also fig. 17). Some of the diagonal band fibres may enter it. Further anteriorly it sweeps round the ventral surface of the tuberculum (figs. 12, 18) and ascends under the pia mater in the anterior part of the paraterminal body to reach the hippocampal formation and perhaps the nucleus olfactorius anterior (fig. 19). It may of course receive fibres from both the anterior part of the paraterminal body and tuberculum as well as from the regions already mentioned.

Stria medullaris medialis. This consists of two divisions which are clearly seen in fig. 16, the median cortico-habenular and median olfacto-habenular tracts.

The medial cortico-habenular tract starts in a tangled network of fibres well seen in figs. 17 and 18 behind and slightly above the anterior commissure.

It is connected by crossed and uncrossed fibres with the anterior and posterior parts of the alveus system. Anteriorly (fig. 15) alveus fibres which are descending in the lateral part of the fornix columns run into this network. Posteriorly fibres enter it from the posterior hippocampal commissure (fig. 18) and directly from the posterior part of the alveus system (fig. 17). It receives also some fibres from the medial part of the central amygdaloid mass (fig. 17, *Amy. hab.*).

The medial olfacto-habenular fibres can be seen in figs. 16 and 17. They run ventrally and fork into a large posterior and a small anterior bundle. The posterior bundle joins the medial fore-brain bundle and goes to the hypothalamus. The anterior bundle runs across the fibres of the medial fore-brain bundle to the preoptic nucleus. Since the hypothalamus belongs to the diencephalon, the posterior bundle should be excluded from the stria medullaris if the definition of the latter is adhered to strictly. From the point of view of the anatomy of the adult brain, this exclusion seems an unnatural one.

This description agrees, except in comparatively minor details, with descriptions of the stria medullaris (the "taenia thalami" of continental writers) in other reptilian orders. Some differences have already been mentioned in the discussion of the paraterminal body (p. 189). It is noteworthy that Cairney failed to find direct cortico-habenular fibres in *Sphenodon*.

The use of the term "tract" for the various medial and lateral cortico- and olfacto-habenular connections seems a little inappropriate since only in a few cases (e.g. the tractus olfacto-habenularis anterior) are there fibres collected into definite tracts. The connections are for the most part diffuse and reach nearly all the medial and lateral cortical and olfactory centres of the hemisphere.

The fore-brain bundles

The fore-brain bundles are large tracts of fibres which connect the telencephalon with the diencephalon and also probably with the mid-brain and perhaps lower centres. Most of their connections have been mentioned already, but it will be convenient here to summarise them, and to consider the tracts as a whole.

In the anterior part of the hemisphere medial and lateral fore-brain bundles can be recognised (fig. 12, *M.F.B.*, *L.F.B.*). The medial bundle lies between the palaeostriatum and the tuberculum. It gives fibres to or receives them from the palaeostriatum and the paraterminal body, and possibly the tuberculum olfactorium. It appears to be connected with all parts of the paraterminal body, some of its fibres sweeping up in front of the commissures (fig. 18) and then back into its supraforaminal part. Others appear to run into direct continuity with the alveus fibres (fig. 13). It would appear to be mainly an efferent tract from the hippocampal cortex and paraterminal body to diencephalic and mid-brain centres, but probably contains ascending fibres as well. It runs back underneath the anterior commissure, where it becomes closely applied to the lateral fore-brain bundle and lies lateral to the preoptic and hypothalamic nuclei and above the optic tract (fig. 14). Most of its fibres run

ventrally as well as caudally (fig. 18), and end in the hypothalamus, together with many fibres from the lateral fore-brain bundle. In this region it is difficult to distinguish medial and lateral bundles (figs. 15, 16). They are very closely applied to one another, and the only differentiation is due to the denser packing of the fibres laterally. Here it would be most accurate to speak of a single fore-brain bundle which, as Cairney has described it in *Sphenodon*, divides into a dorsal and a ventral peduncle (fig. 17, *Ped. dor.*, *Ped. vent.*). The dorsal peduncle consists of rather coarse fasciculi, probably wholly and certainly mostly derived from the lateral fore-brain bundle. It runs to the thalamus. The ventral peduncle consists probably of all the medial fore-brain bundle and quite a large contribution from the lateral, and runs caudally as well as ventrally. Many fibres undoubtedly end in the hypothalamus, while others run in to the ventral part of the mid-brain and perhaps to lower centres.

The medial fore-brain bundle receives contributions from several other fibre tracts, mostly running to the hypothalamus. These are: (i) alveus fibres anterior to the commissures which have been mentioned already. Other alveus fibres descend between the components of the anterior commissure and still more posterior to them (columns of fornix), and all run with the bundle towards the hypothalamus (figs. 13–15). (ii) The stria terminalis fibres from the amygdaloid complex which arch over the fore-brain bundle and descend with the medial bundle to the hypothalamus (fig. 15). (iii) A strong contribution from the tractus olfacto-habenularis medialis (p. 201 and fig. 17).

The lateral fore-brain bundle consists of coarser fasciculi than the medial and begins a little further forward. It collects fibres from the anterior two-thirds of the hypopallium anterior, from the edge of the dorsal cortex where it bends round to join the hypopallium (the "primordium neopallii") and from the lateral part of the palaeostriatum (the "somatic striatum") through which it runs. Anteriorly (figs. 12, 13) it is fairly clearly distinguishable from the medial fore-brain bundle, and between them the olfactory component of the anterior commissure lies. Its ultimate fate has already been mentioned in describing the dorsal and ventral peduncles. Which particular fibres go to the thalamus and which to the hypothalamus and lower centres it is impossible to say.

It is clear then, that the medial fore-brain bundle is chiefly a tract connecting olfactory centres, the hippocampus and paraterminal body with the hypothalamus. It has also connections with the medial part of the palaeostriatum which may be an olfactory centre (the "olfacto-striatum"). The lateral fore-brain bundle is a link between the thalamus, the hypopallium anterior, and a small part of the dorsal cortex and the lateral part of the palaeostriatum. It has hypothalamic connections as well, and probably both bundles are connected to the mid-brain and perhaps lower centres.

It is very difficult to assess the functional importance of these bundles because of the lack of knowledge of the direction of conduction in them. There is reason to suppose that the alveus is efferent from the hippocampus, which makes it probable, but not certain, that the medial fore-brain bundle contains

mostly descending fibres. It would seem likely too, that the lateral fore-brain bundle should contain mostly ascending sensory fibres from the thalamus to the striatum, hypopallium, and cortex, but again the possibility that many fibres are descending to the hypothalamus and mid-brain cannot yet be affirmed or denied.

Very similar descriptions of the fore-brain bundles have been published by American writers, who have used this same terminology. Edinger has used the term "basal fore-brain bundle" for the lateral bundle alone, with the alternative term "tractus strio-thalamicus." In the continental literature the medial bundle is commonly referred to as the "tractus septo-mesencephalicus." The terms "medial" or "lateral" fore-brain bundle seem more satisfactory, since the connections of each are too varied for an accurate and convenient term to be coined which can indicate them. The term "tractus septo-mesencephalicus," for example, is applicable only to some of the fibres which run in the medial fore-brain bundle.

A connection between the thalamus and the antero-lateral part of the dorsal cortex (primordium neopallii) seems to be very general. It has been described in the turtle (Johnston), chameleon (Shanklin), alligator (Crosby), gecko (Unger), *Varanus* (de Lange). The last two writers use the term "tractus fronto-thalamicus" for these fibres. De Lange suggests that the connection is rather with the dorsal part of the pyriform cortex than with the dorsal cortex (his "cortex ammonis"), but his figures do not support this contention.

In *Lacerta* the division of both bundles into dorsal and ventral peduncles is similar to that described by Kappers (1921) and Cairney (1926). Shanklin (1930) states that in the chameleon it is only the lateral bundle which divides in this way. He described mid-brain connections for the lateral bundle (ventral peduncle) in considerable detail. In general my findings agree with his, but the material is not adequate for the investigation of mid-brain connections in detail.

The direction of conduction in these bundles is clearly a matter of importance. Probably it occurs in both directions, with the medial bundle mainly descending and the lateral mainly ascending. Crosby, on the strength of Golgi preparations, finds evidence for conduction in both directions in both bundles in the alligator. This applies also to the cortical connections of the lateral bundle, although it appears that the descending fibres from the dorsal (general) cortex are relayed in the striatum. In view of the possibility that this region of the dorsal cortex is a "primordium neopallii," the presence and destination of these descending fibres is of considerable interest and worthy of further investigation. Experimental lesions with a study of the tract degenerations resulting from them would appear to be the best means of attacking this problem.

CONCLUSION

A discussion and summary of findings in a paper of this kind cannot be of much value, since the work is mainly concerned with the investigation and correlation of detail. On the whole my observations in *Lacerta* agree very

closely with those of others in different members of the same order and in the other different orders of reptiles. The agreement with Cairney's and Durward's descriptions of *Sphenodon* is particularly close.

One of the most striking features of the lacertilian brain is the characteristic development of the hypopallium posterior. In this it is unlike the Rhyncocephalia, Crocodilia, or Chelonia, but like the Ophidia. It appears to be associated with a comparative lack of differentiation in the remaining part of the amygdaloid complex in which Johnston, Crosby and Durward have described definite nuclear masses in the turtle, alligator, and *Sphenodon* respectively.

For a Reptile, cortical differentiation has reached a fairly high level in the Lacertilia, and the presence of commissural fibres from the dorsal cortex in the anterior commissure is a fresh point which suggests the comparison of this cortical region with the neopallium of prototherian Mammals. The question of the presence or absence of these fibres in other Reptiles deserves investigation.

The corpus striatum is typically reptilian. It does not reach the high degree of development seen in the alligator. Compared with the other reptilian orders, the differences are not great, and their significance is obscure.

It seems probable that the structure of the paraterminal body is very uniform throughout the whole class, the most striking difference being due to the presence or absence of a posterior hippocampal commissure with the concomitant presence or absence of a well-developed supraforaminal part of the paraterminal body. The paraterminal body of the opossum (Loo, 1931), and of the Macroscelididae (Le Gros Clark, 1928), appears to be built on the same plan. A re-investigation of the paraterminal body in the Chelonia and Crocodilia with a view to revision of terminology is desirable.

Detail, such as the methods used here can disclose, is still rather meagre concerning the fibre connections in the fore-brain of the Chelonia, and concerning the general anatomy of the ophidian brain. Further investigation in these fields and by these methods may therefore be expected to yield interesting results. Some of the differences between Cairney's description of fibre connections in *Sphenodon* and descriptions in other forms, may be due to his lack of good silver preparations. Further embryological investigations in all orders, and particularly in the region of the corpus striatum and amygdaloid, are clearly needed. The work which has been done already leaves one with the impression that the embryological method may not throw much light on the outstanding morphological problems, but obviously it needs application in a wider field before its limitations can be assessed. The experimental method, or the study of the degenerations resulting from controlled injuries, seems to offer more hope of definite information, particularly so far as the olfactory and cortical connections are concerned. Its findings might usefully be controlled, particularly in the region of the cortex, by a detailed study of Golgi and Cox-Golgi preparations, or by any method which renders both the cell body, axon and dendrites visible in one and the same preparation.

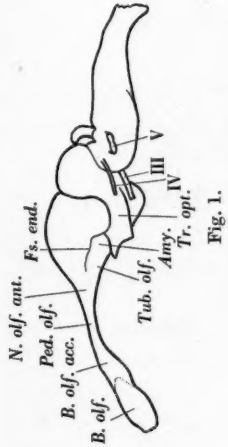

Fig. 1.

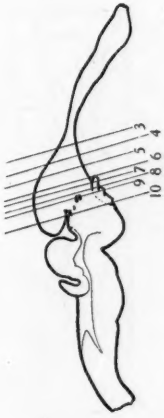

Fig. 2*a*.

Fig. 2*b*.

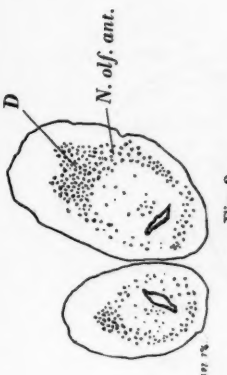

Fig. 3.

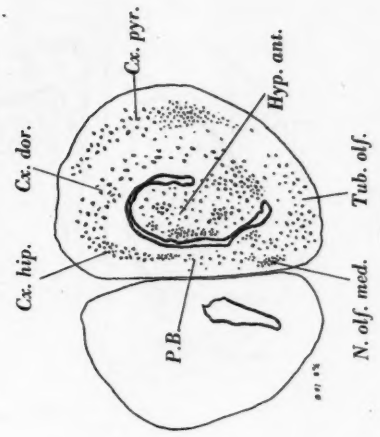

Fig. 4.

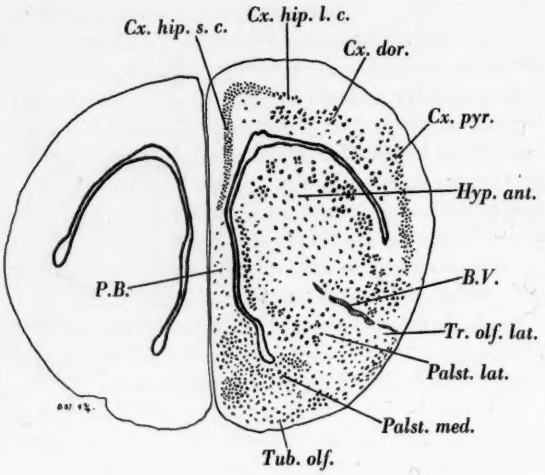
Cx. hip. s. c.
Cx. hip. l. c.
Cx. dor.
Cx. pyr.
Hyp. ant.
P.B.
B.V.
Tr. olf. lat.
Palst. lat.
Palst. med.
Tub. olf.

Fig. 5.

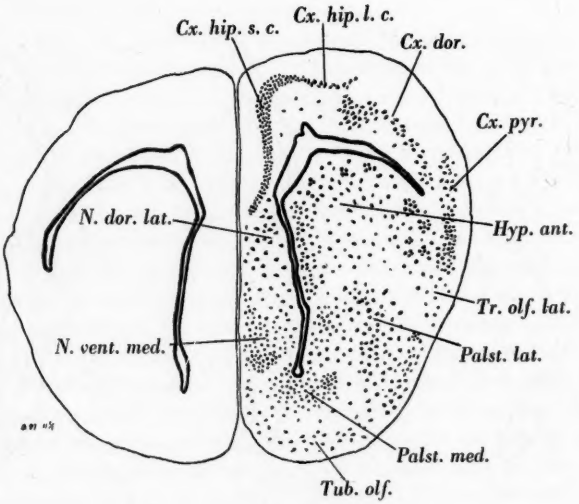
Cx. hip. s. c.
Cx. hip. l. c.
Cx. dor.
Cx. pyr.
N. dor. lat.
Hyp. ant.
Tr. olf. lat.
N. vent. med.
Palst. lat.
Palst. med.
Tub. olf.

Fig. 6.

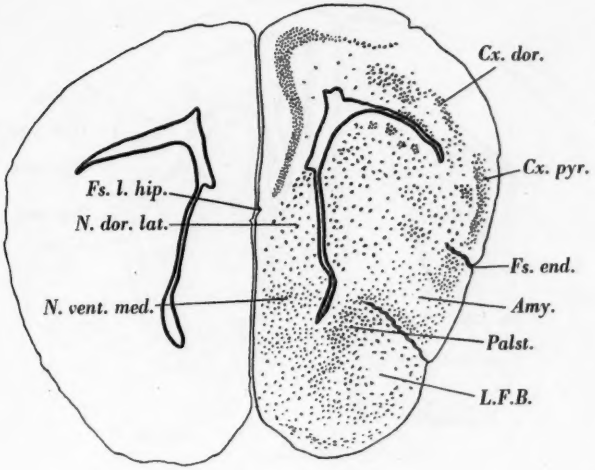
Cx. dor.
Cx. pyr.
Fs. l. hip.
N. dor. lat.
Fs. end.
N. vent. med.
Amy.
Palst.
L.F.B.

Fig. 7.

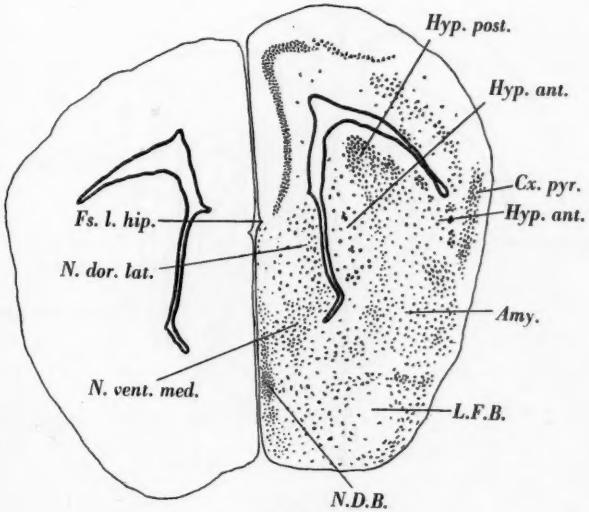
Hyp. post.
Hyp. ant.
Cx. pyr.
Hyp. ant.
Fs. l. hip.
N. dor. lat.
Amy.
N. vent. med.
L.F.B.
N.D.B.

Fig. 8.

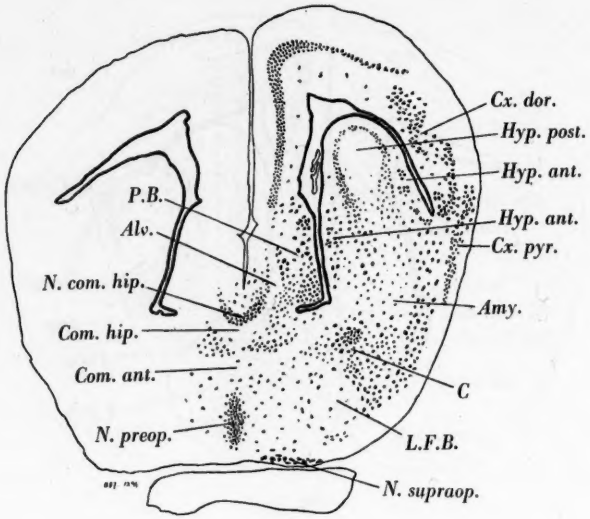
Cx. dor.
Hyp. post.
Hyp. ant.
P.B.
Alv.
Hyp. ant.
Cx. pyr.
N. com. hip.
Amy.
Com. hip.
Com. ant.
C
N. preop.
L.F.B.
N. supraop.

Fig. 9.

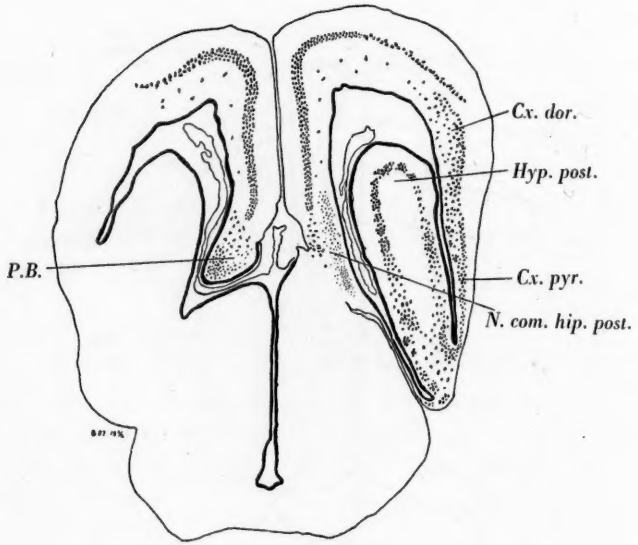
Cx. dor.
Hyp. post.
P.B.
Cx. pyr.
N. com. hip. post.

Fig. 10.

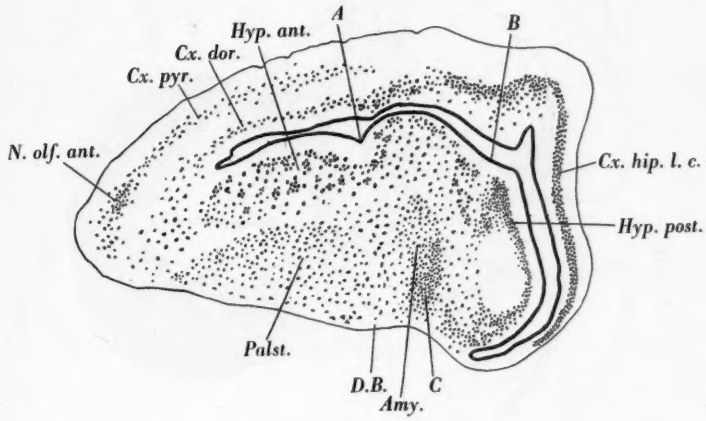
A
Hyp. ant.
B
Cx. dor.
Cx. pyr.
N. olf. ant.
Cx. hip. l. c.
Hyp. post.
Palst.
D.B.
Amy.
C

Fig. 11.

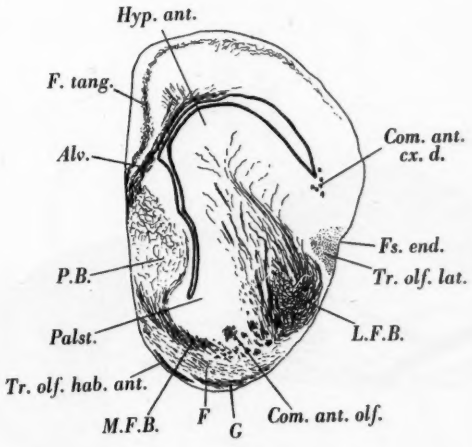
Hyp. ant.
F. tang.
Com. ant.
cx. d.
Alv.
Fs. end.
P.B.
Tr. olf. lat.
Palst.
L.F.B.
Tr. olf. hab. ant.
M.F.B.
F
G
Com. ant. olf.

Fig. 12.

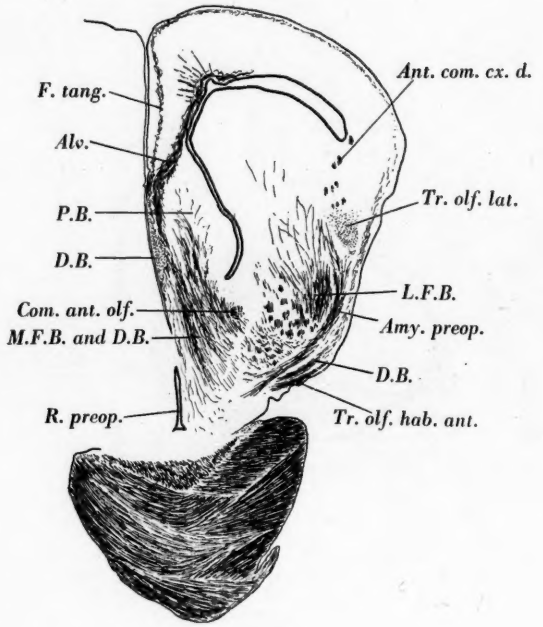
F. tang.
Alv.
P.B.
D.B.
Com. ant. olf.
M.F.B. and D.B.
R. preop.
Ant. com. cx. d.
Tr. olf. lat.
L.F.B.
Amy. preop.
D.B.
Tr. olf. hab. ant.

Fig. 13.

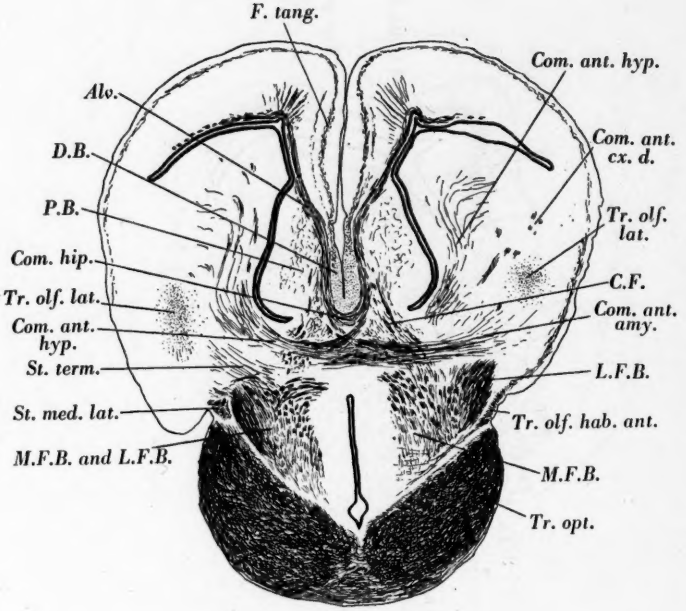
F. tang.
Alv.
D.B.
P.B.
Com. hip.
Tr. olf. lat.
Com. ant. hyp.
St. term.
St. med. lat.
M.F.B. and L.F.B.
Com. ant. hyp.
Com. ant. cx. d.
Tr. olf. lat.
C.F.
Com. ant. amy.
L.F.B.
Tr. olf. hab. ant.
M.F.B.
Tr. opt.

Fig. 14.

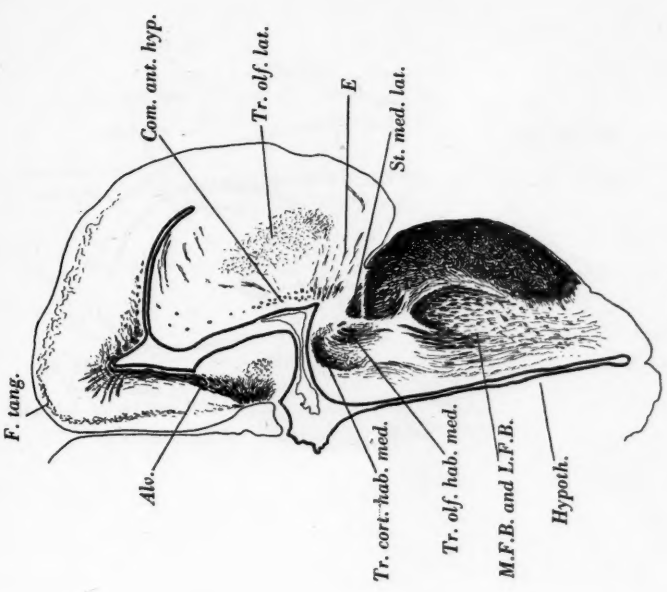
F. tang.
Alv.
Com. ant. hyp.
Tr. olf. lat.
E
St. med. lat.
Tr. cort. hab. med.
Tr. olf. hab. med.
M.F.B. and L.F.B.
Hypoth.

Fig. 16.

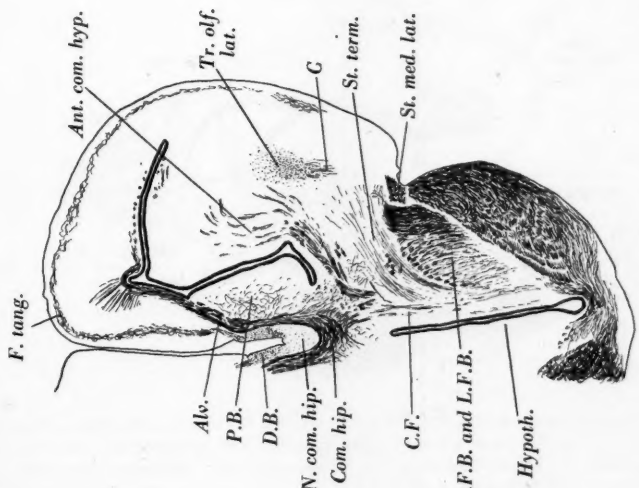
F. tang.
Ant. com. hyp.
Tr. olf. lat.
C
St. term.
St. med. lat.
Alv.
P.B.
D.B.
N. com. hip.
Com. hip.
C.F.
M.F.B. and L.F.B.
Hypoth.

Fig. 15.

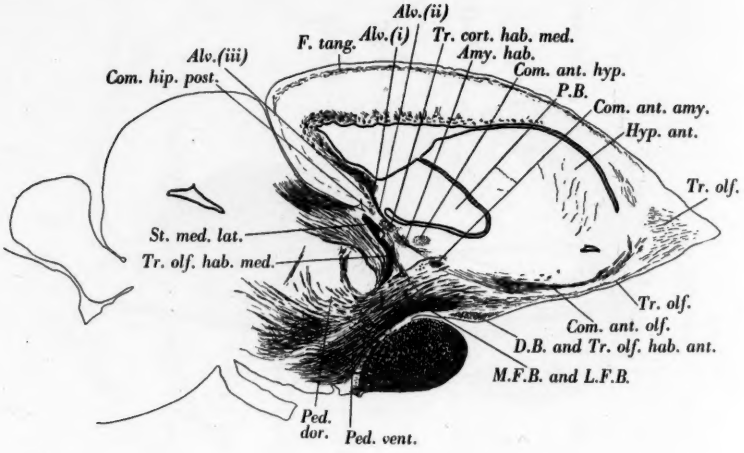
Alv.(ii)
Alv.(i)
F. tang.
Tr. cort. hab. med.
Alv.(iii)
Amy. hab.
Com. hip. post.
Com. ant. hyp.
P.B.
Com. ant. amy.
Hyp. ant.
Tr. olf.
St. med. lat.
Tr. olf. hab. med.
Tr. olf.
Com. ant. olf.
D.B. and Tr. olf. hab. ant.
M.F.B. and L.F.B.
Ped. dor.
Ped. vent.

Fig. 17.

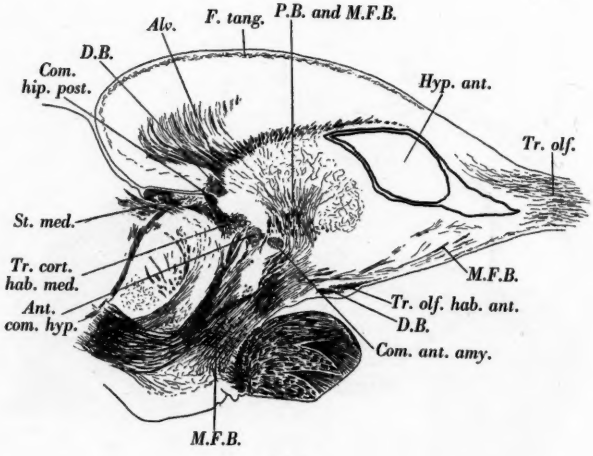
Alv.
F. tang.
P.B. and M.F.B.
D.B.
Com. hip. post.
Hyp. ant.
Tr. olf.
St. med.
Tr. cort. hab. med.
M.F.B.
Ant. com. hyp.
Tr. olf. hab. ant.
D.B.
Com. ant. amy.
M.F.B.

Fig. 18.

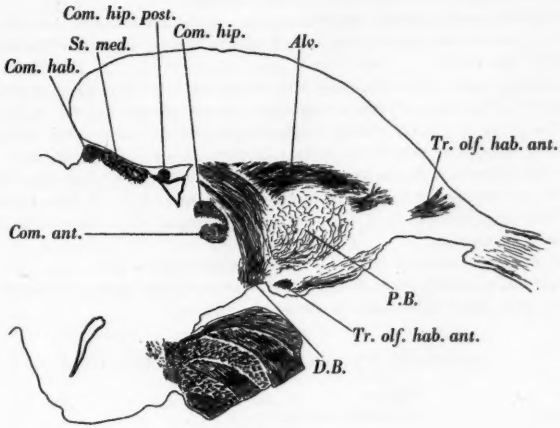

Fig. 19.

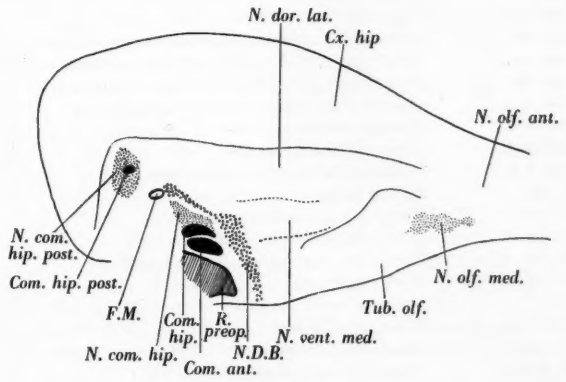

Fig. 20.

All the figures, with the exception of figs. 1 and 2*a* and *b*, which were traced from photographs, and fig. 20, which is a graphical reconstruction, were drawn in outline from the sections with Edinger's projection apparatus. Detail was added afterwards with the aid of a microscope. The magnifications of figs. 1 and 2*a* and *b* are × 5, of figs. 3–16, × 35 and of figs. 17–20, × 23.

LEGENDS TO TEXT-FIGURES

Fig. 1. Sketch of lateral aspect of brain of *Lacerta viridis*.

Figs. 2 *a* and *b*. Sketch of a medial sagittal section of the same brain. In *a* the approximate position and plane of the sections from which figs. 3–10 were drawn is indicated. The same is done in *b* for figs. 12–16.

Figs. 3–10. Drawings made from a transverse series stained with toluidin blue (series B 87). The indication of relative sizes of cells is only approximate and the number of cells is very much larger in the actual specimen. Owing to the obliquity of the sections, the left-hand side of the figure (partly completed only in fig. 10) is slightly anterior to the right.

Fig. 11. Parasagittal section drawn from a specimen stained with toluidin blue (series B 99).

Figs. 12–16. Transverse sections drawn from the Bielschowsky series B 102. In these figures the left-hand side (completed in fig. 14) is posterior to the right. The relative thickness of fibres is not indicated accurately.

Figs. 17–19. Parasagittal sections from the Bielschowsky series B 109.

Fig. 20. A graphical reconstruction showing the position of structures in relation to the medial hemisphere wall. Made from series B 87.

ABBREVIATIONS USED IN FIGURES

Alv.	Alveus.
Amy.	Amygdala (central mass).
Amy. hab.	Amygdalo-habenular fibres.
Amy. preop.	Amygdalo-preoptic fibres.
Ant. com. cx. d.	See *Com. ant. cx. d.*
Ant. com. hyp.	See *Com. ant. hyp.*
B. olf.	Bulbus olfactorius.
B. olf. acc.	Bulbus olfactorius accessorius.
B.V.	Blood vessel.
C.F.	Columna fornicis.
Com. ant.	Commissura anterior.
Com. ant. amy.	Commissura anterior, amygdaloid component.
Com. ant. cx. d.	Fibres from the dorsal cortex to the anterior commissure.
Com. ant. hyp.	Commissura anterior, hypopallial component.
Com. ant. olf.	Commissura anterior, olfactory component.
Com. hab.	Commissura habenularis.
Com. hip.	Commissura hippocampi.
Com. hip. post.	Commissura hippocampi posterior.
Cx. dor.	Cortex dorsalis.
Cx. hip.	Cortex hippocampi.
Cx. hip. l. c.	Cortex hippocampi, large-celled part.
Cx. hip. s. c.	Cortex hippocampi, small-celled part.
Cx. pyr.	Cortex pyriformis.
D.B.	Diagonal band.
F.M.	Foramen of Monro.
Fs. end.	Fissura endorhinalis.
Fs. l. hip.	Fissura limitans hippocampi.
F. tang.	Fibrae tangentiales.
Hyp. ant.	Hypopallium anterior.
Hyp. post.	Hypopallium posterior.
Hypoth.	Hypothalamus.
L.F.B.	Lateral fore-brain bundle.
M.F.B.	Medial fore-brain bundle.
N. com. hip.	Nucleus commissurae hippocampi.
N. com. hip. post.	Nucleus commissurae hippocampi posterior.
N.D.B.	Nucleus of the diagonal band.
N. dor. lat.	Nucleus dorso-lateralis of paraterminal body.
N. olf. ant.	Nucleus olfactorius anterior.

N. olf. med.	Nucleus olfactorius medialis.
N. preop.	Nucleus preopticus.
N. supraop.	Nucleus supraopticus.
N. vent. med.	Nucleus ventro-medialis of paraterminal body.
Palst.	Palaeostriatum.
Palst. lat.	Palaeostriatum, lateral part.
Palst. med.	Palaeostriatum, medial part.
P.B.	Paraterminal body.
Ped. dor.	Pedunculus dorsalis.
Ped. olf.	Pedunculus olfactorius.
Ped. vent.	Pedunculus ventralis.
R. preop.	Recessus preopticus.
St. med.	Stria medullaris.
St. med. lat.	Stria medullaris lateralis.
St. term.	Stria terminalis.
Tr. cort. hab. med.	Tractus cortico-habenularis medialis.
Tr. olf.	Tractus olfactorius.
Tr. olf. hab. ant.	Tractus olfacto-habenularis anterior.
Tr. olf. hab. med.	Tractus olfacto-habenularis medialis.
Tr. olf. lat.	Tractus olfactorius lateralis.
Tr. opt.	Tractus opticus.
Tub. olf.	Tuberculum olfactorium.

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THE BRAIN OF THE KENYA NATIVE

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Medical Research Laboratory, Kenya

THIS communication is a record of macroscopical and microscopical examination of 100 brains of Kenya natives.

The indigenous population of the Colony is said to be a mixture of Negroid and Hamite stocks. Their physique is poor; that of the Kikuyu, from which tribe 48 per cent. of the material was obtained, has been described by Orr and Gilks as follows:

"The physique of the typical male Kikuyu may be judged from recruiting statistics (Tate, 1917–18). Of the 16,754 men of one district of the Reserve who were called up during 1917 for enrolment in the Carrier Corps, 10,912 were immediately rejected on medical grounds. Following the march of one hundred miles to the depôt at Nairobi, a further 17 per cent. were rejected as physically unfit."

Whether or not this description still holds good for the average native nevertheless, diseases common to other climates are as prevalent amongst the native population as diseases peculiar to the tropics. The high incidence of spirochaetal diseases, yaws and syphilis, must be taken into consideration in any deductions drawn from the findings in this series of brains. Spirochaetal diseases are stated not to affect the central nervous system of Africans, but an investigation just carried out by Dr H. L. Gordon, and my own experience of post-mortem work, do not support this belief for Kenya.

The material used was obtained at autopsies carried out personally in the native hospitals of Nairobi, but does not include cases from the prisons or the Mental Hospital. Only brains that appeared to be normal were used, and were all from adult males. An adult male was regarded as being one of 18 years of age or more. The 100 cases investigated were as follows:

Kikuyu (Bantu)	48
Kavirondo (Bantu)	16
Jaluo (Nilotic)	15
Wakamba (Bantu)	11
Other tribes	10

These 100 brains represent the average native population, but do not include any of the so-called educated class. The educated native is generally the product of the mission schools, and in my experience he is rarely seen on the post-mortem table.

METHODS

On removal of the brain from the body it was weighed without removal of the meninges. It was then suspended by the basilar arteries in 10 per cent. formol saline, care being taken that the brain did not touch the sides or

bottom of the container. Owing to climatic and other local conditions, it was impossible to fix the brain by injection of the carotid arteries.

The preparation of microscopic specimens was as follows. After sectioning, the tissue was carried through the various grades of alcohol, cleared in xylol, and embedded in paraffin wax. Sections were cut at 25μ, taken through xylol and alcohol, to water, and then washed in two changes of distilled water for at least 2 hours. They were then stained for 24 hours, preferably in the dark, in the following solution:

Giemsa's stain	...	...	1·25 c.c.
Methyl alcohol	...	...	1·75
Distilled water	...	...	47·00

On removal from the stain the sections were washed in distilled water and transferred to methyl alcohol containing one drop of 10 per cent. colophonium to every c.c. To obtain even differentiation the sections were kept in constant motion in this solution. They were then passed rapidly through absolute alcohol, placed on slides, blotted and mounted in Gurr's neutral mounting medium. The resulting preparations showed blue-stained nerve cells on a pink background.

WEIGHT OF THE BRAIN

In a series of 389 apparently normal adult male native brains, the average weight was 1276 gm. or 45 oz., the extremes being 1006 gm. and 1644 gm. The weights were taken immediately the brain had been removed from the body with the arachnoid and pia mater *in situ*, and the ventricles full.

Mathews states that the density of the whole brain is 1·037; using this figure the average volume of the native brain is 1230 c.c. In a small series of cases I have estimated the average volume by means of water displacement, and this figure appears to be correct.

The figures given by different authors for the average weight of the brain in white races vary considerably. Shennan gives 1428 gm. as the average of Gray, Cunningham, Luschka, Krause and Neuwerck. If this is the average weight of the European brain, then the average brain of the African native is 152 gm. or 10·6 per cent. lighter.

My post-mortem records suggested that the brain of the native youth is as heavy as that of the adult. Therefore the average weight was calculated by age groups, for those cases in which the age was known, as follows:

Age group Years	No. of cases	Average weight gm.
9–15	29	1301
16–20	74	1279
21–25	87	1270
26–30	69	1264
31–35	24	1262
36–40	13	1256
41 and over	28	1230

From these figures it would appear that the native brain reaches its full weight prior to the age of 18 years, and that there is evidence of decrease after the age of 40.

Some anthropological significance has been attached to the relative weights of the fore-brain and the mid- and hind-brain. Tilney gives the following figures for the human race:

Fore-brain	... ...	86–89 %
Mid-brain	... 1 %	... 11–14 %
Hind-brain	... 10–13 %	

In this series, the average percentages were:

Fore-brain	87·2 %
Mid-brain and hind-brain	12·8 %

These figures for the mid- and hind-brain, as in the case of the whole brain, were obtained from the fresh specimens without the removal of the leptomeninges.

These percentages for the native indicate no significant variation from those of Tilney, but show a uniform reduction in the weight of the different portions of the brain.

THE MACROSCOPIC APPEARANCES OF THE LEFT HEMISPHERE OF 100 BRAINS

General form. Viewed from the side, the upper border of the native brain had a flattened appearance; seen from above the frontal lobes it had a rectangular shape. In the parietal region there was a pronounced increase in width of the brain. The temporal lobes appeared to be narrower than in the European brains used for comparison, and the temporal pole was blunted and turned inwards. All the brains examined showed a pronounced rostrum orbitale. The degree of exposure of the insula varied considerably from brain to brain, being well marked in 34 brains and less marked in 26.

Convolutional pattern. The convolutional pattern differed somewhat from that of the European. Identification of the individual sulci, especially in the frontal region, seemed to me relatively easier in the native.

The *central sulcus* in 14 per cent. of the cases of this series arose on the medial surface of the hemisphere, and in 34 per cent. on the lateral surface. This fissure had not the sinuous course seen in the European, but tended to be straight with poorly developed genua. In 26 per cent. of the cases it reached the Sylvian fissure.

In 22 cases the *lateral cerebral fissure* (fissure of Sylvius) had one ramus absent or represented by a mere indentation of the cortex of the brain. In general the ascending ramus was situated in close proximity to the inferior portion of the precentral sulcus. Posteriorly the Sylvian fissure passed into the parietal lobe, and in 12 of the brains cut through the supramarginal gyrus to end in the intraparietal sulcus.

The *precentral sulcus* in 14 brains was shown as a continuous fissure, and in 17 cases was divided into three portions. It tended to join the Sylvian either directly or through the anterior subcentral fissure.

The *superior* and *inferior frontal sulci* generally were found to arise in the precentral sulcus, and were often seen as small, broken fissures. The *sulcus frontalis medius* (Eberstaller) was well defined; in 43 cases it arose in the precentral sulcus and passed forward usually as a continuous sulcus to end in the fronto-marginal. The *sulcus radiatus* was present in all the brains examined, but the *sulcus diagonalis*, the *sulcus subcentralis anterior*, and the *paramedians* were variable.

The *superior temporal sulcus* was continuous in 76 of the brains, and on the whole started rather far back in the temporal lobe. The *middle* and *inferior temporal sulci* were poorly developed, being seen as small discontinuous fissurettes. The *rhinal sulcus* tended to a straight course, but occasionally was boldly curved.

In 51 of the brains the *intraparietal sulcus* commenced in the post central sulcus. In all brains it rose rapidly towards the upper border to pass backwards, and end in the transverse occipital fissure. In 24 brains it was divided into its component parts.

A *lunate sulcus* is a common finding in the African brain, being present in 70 of the brains of this series. In these 70 it was well developed in 54, and to a lesser degree in 16.

In 10 brains the *calcarine fissure* lay entirely on the medial surface of the hemisphere; in 32 the lateral portion was separated from the rest of the fissure. The *paracalcarine fissure* was, on the whole, poorly developed. It is noteworthy that the parieto-occipital fissure in one brain did not reach as far as the medial border of the hemisphere, while in 23 brains it passed through the arcus parieto-occipitalis to end in the intraparietal fissure.

ANTHROPOMETRY

Measurements of the head of the East African by Dr H. L. Gordon show it to be dolichocephalic, the length/breadth index calculated on 1000 male adults of all tribes being 74·8. The degree of dolichocephaly varies with the tribe under examination, and this must affect the indices of a series of brains derived from different tribes. Nevertheless, indices have been prepared from 12 consecutive brains according to the method of Kappers. The following are the average figures:

Height index	0·462
Occipital index	1·093
Temporal depth index	0·130
Temporal length index	0·749
*Frontal height index	1·594
*Frontal length index	0·251
Callosal index	0·295

* These two indices are Kapper's original ones, i.e. frontal height index = insular perpendicular divided by its distance from the frontal pole, and the frontal length index = distance from the insular perpendicular to the frontal pole, divided by the lateral horizontal.

The indices depending on height measurements are smaller in the native brain than in Kappers' series of Dutch dolichocephalic brains, and yet the degree of dolichocephaly of the native head is anything but marked. Therefore, it is possible to conclude that any failure of development of the native brain is shown in the height. The same conclusion can be drawn concerning the temporal lobe.

MICROSCOPIC APPEARANCES

Bolton, dealing with the subject of cortical measurements, stresses particularly that his measurements are the average of the depths of the laminae in four regions of the convolution, the flat external surface, the fissure lips, the sides of the fissure and the bottom of the fissure. Von Economo, on the other hand, while pointing out that the crown of the gyrus possesses a cortical lamination twice as thick as the floor of the sulcus, does not mention whether his measurements are obtained in the same manner as Bolton's, or whether they are taken only from the flat external surface of the gyrus. The total of his measurements of the laminae in each area lie within the limits given in his "Table of cortical thickness of the crowns of the gyri of the most important areas." It was assumed from this that the measurements given by this author were taken from the crown or flat external surface, and on this assumption the measurements of the native cortex, which are taken from the crown or flat external surface of the gyrus, are compared in Table I with the figures given by Von Economo for the corresponding areas of the European brain. The measurements of the native cortex given in the table are the average for the brains of this series, and in each case the sections were taken from the left hemisphere of the brain. The portion of cortex from which the sections were prepared is shown in figs. 2 and 3.

The average total reduction of the whole cortex as compared with the European in the areas examined is 14·8 per cent.

Woollard states that in the precentral motor area of the brain of the Australian aboriginal the internal granular layer, though reduced in size, is a more marked remnant than in the white brain. In the African, while there is definitely a remnant of this internal granular layer present, it does not appear to be more marked than in the European. On the other hand, the pyramidisation of the cells in this area of the African brain is not so complete. In the motor area there is another significant fact. Betz cells are less conspicuous than in the European; they appear to be fewer in number and are definitely smaller in size. Von Economo gives the measurements for Betz cells as $\frac{60-120\mu}{30-60\mu}$. In the native cortex the size is $\frac{45-90\mu}{25-45\mu}$. Giant pyramidal cells were not found in sections taken from the intermediate precentral area (area 6). The striated appearance which is so noticeable in some areas of the European cortex is not so well shown in the native brain.

The cortical measurements of the native show that, except in the visuosensory area (area 7), the lamina zonalis is in every case greater than in

the European brain, whereas the measurement of the supragranular layer is smaller. This appears to be in keeping with the statement of Kappers:

"The space between the surface and the granular layer originally is an important region for corticopetal impulses. It is not strange that these impulses

Table I. *Cortical measurements*

Area	Laminae	Measurement in mm.	% increase or decrease compared with the European brain
1 (F.E.)	Zon.	0·251	+14
	Supragran.	0·665	−11
	Gran. int.	0·216	−28
	Infragran.	1·049	− 5
	Total	2·181	− 9
2 (F.B.)	Zon.	0·242	+10
	Supragran. + Gran. int.	0·963	−36
	Infragran.	1·625	−14
	Total	2·830	−20
3 (F.A.)	Zon.	0·226	+25
	Supragran. + Gran. int.	1·127	−25
	Infragran.	1·653	−21
	Total	3·006	−21
4 (P.C.)	Zon.	0·231	+ 5
	Supragran.	0·832	−26
	Gran. int.	0·260	−26
	Infragran.	1·136	*
	Total	2·459	−22
5 (T.A.)	Zon.	0·232	+ 5
	Supragran.	0·922	−12
	Gran. int.	0·171	− 5
	Infragran.	1·333	− 5
	Total	2·658	− 7
6 (F.D.C.)	Zon.	0·202*	.
	Supragran.	0·700*	.
	Gran. int.	0·181*	.
	Infragran.	0·944*	.
	Total	2·027	−19
7 (O.C.)	Zon.	0·181	− 5
	Supragran.	0·338	−14
	Gran. int.	0·600	−25
	Infragran.	0·766	+14
	Total	1·886	− 8
8 (O.A.)	Zon.	0·195	+ 8
	Supragran.	0·671	−19
	Gran. int.	0·200	− 0
	Infragran.	0·868	−18
	Total	1·978	−13

The letters in brackets are Von Economo's areas.

* No details of these laminae are given by Von Economo, and the total width of the cortex in these cases is taken from his "Table of cortical thickness."

give rise to a much greater outgrowth of matrix cells of the granular layer in a superficial direction, and thus to the formation of the supragranular cell layers which, in maturing, at the same time acquire a larger size."

In connection with this statement it is interesting to note that the average

measurements of the pyramidal cells of the supragranular layer of the African brain are smaller than in the corresponding areas of the European brain. There has been some evidence in this series of native brains to show that the average size of the pyramidal cells in individual brains bears a direct relationship to the width of the layer in question. It is hoped to investigate this question further.

The increase in thickness of the infragranular layer in the visuo-sensory area is worthy of note.

Cell counts carried out on sections from the different portions of the brains examined failed to show a diminution in the number per unit area, as compared with the brain of the European. Any apparent reduction assumed from inspection of photographs is attributable to the cells being smaller in the native brain, and by the fact that many of the cells are only slightly differentiated. Woollard, on the contrary, found that the closeness of packing, the degree of differentiation and the size of the cells, were much the same in the Australian aboriginal and the European brains.

For the whole brain the average ratio of the supragranular layer to the infragranular layer is 5:8. The average ratio of the figures of Von Economo for the same areas is 6:8.

In an endeavour to check the figures in the foregoing table, measurements according to Bolton's method were carried out on the prefrontal, visuo-sensory and visuo-psychic cortices. The results obtained by this method of measurement, on comparison with Bolton's figures, showed no significant deviation from the results already given.

SUMMARY

1. The average weight of the brain of the Kenya native is 10·6 per cent. or 152 gm. less than the average weight given for the brain of the European.

2. No disproportion was found in the percentage weights of the fore-brain and the mid- and hind-brain in the native.

3. A lunate sulcus was present in 70 per cent. of the brains examined, and there was a tendency to exposure of the insula.

4. The reduction in size of the native brain, as compared with the European, seems to be accounted for mainly by a failure in development in height.

5. The cortex of the native brain was found to be narrower than that of the European. This is true of all the individual laminae in the areas examined, except in the lamina zonalis, and in laminae 5 and 6 of the visuo-sensory area.

6. The pyramidal cells of the supragranular cortex, and the Betz cells of the motor area, are smaller in the native brain than in the European.

7. Cell counts per unit area are the same in the African and European brains.

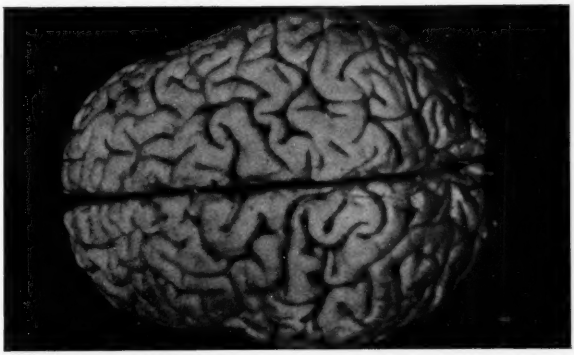

Fig. 1

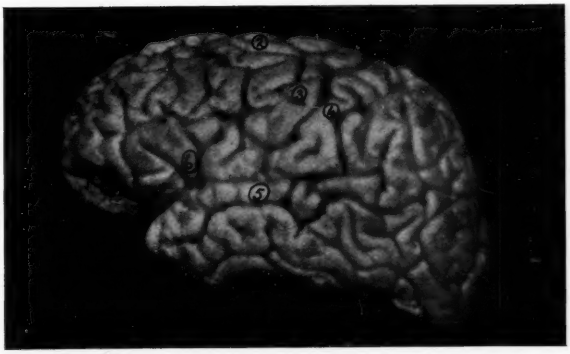

Fig. 2

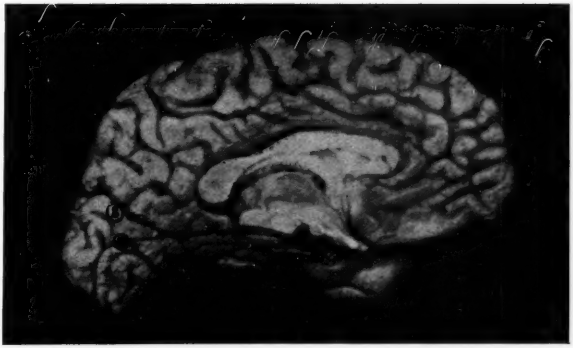

Fig. 3

BRAIN BIOL.

Fig. 4

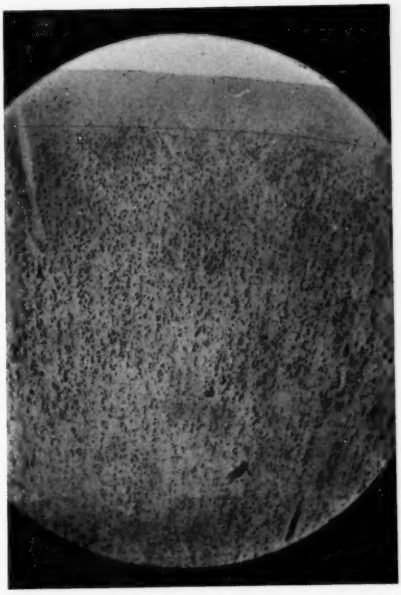

Fig. 5

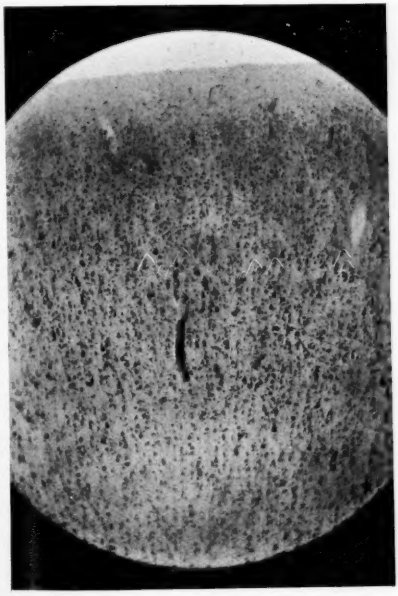

Fig. 6

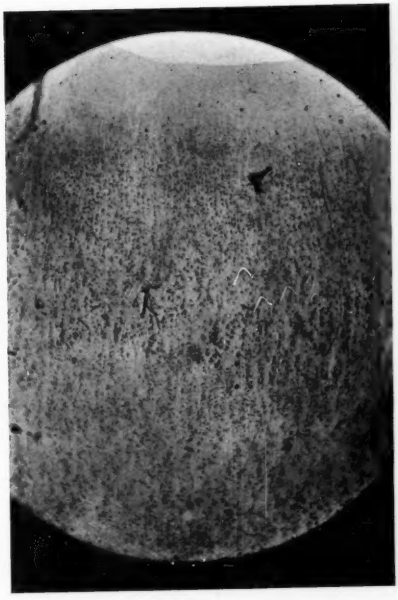

Fig. 7

VINT—The Brain of the Kenya Native

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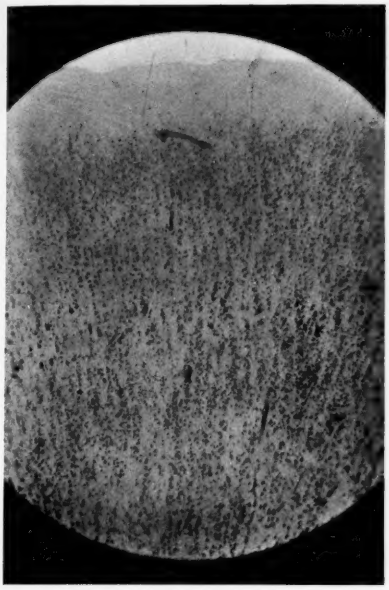

Fig. 8

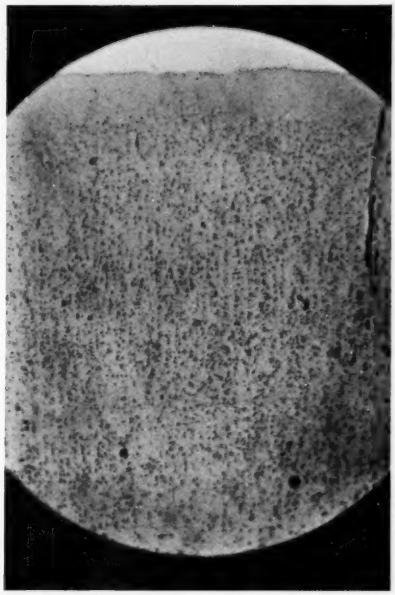

Fig. 9

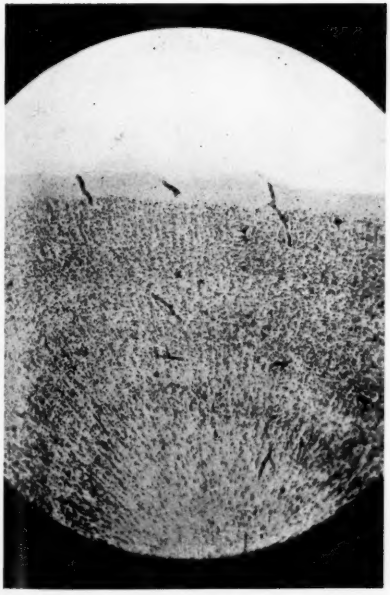

Fig. 10

Fig. 11

VINT—The Brain of the Kenya Native

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EXPLANATION OF PLATES I–III

Plate I

Fig. 1. Typical Kenya native brain viewed from above.
Fig. 2. Lateral aspect of the same brain.
Fig. 3. Medial aspect of the left hemisphere of the same brain.

Plate II

Fig. 4. Area fronto-polaris of a native brain. Area 1 in fig. 2. ×32.
Fig. 5. Area frontalis agranularis of a native brain. Area 2 in fig. 2. ×32.
Fig. 6. Area pre-centralis of a native brain. Area 3 in fig. 2. ×32.
Fig. 7. Area post-centralis of a native brain. Area 4 in fig. 2. ×32.

Plate III

Fig. 8. Area temporalis superior of a native brain. Area 5 in fig. 2. ×32.
Fig. 9. Area pars triangularis of a native brain. Area 6 in fig. 2. ×32.
Fig. 10. Area striata of a native brain. Area 7 in fig. 3. ×32.
Fig. 11. Area peristriata of a native brain. Area 8 in fig. 3. ×32.

DISCONTINUITIES IN THE NORMAL FIELD OF VISION

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PART I. THE FILLING-IN OF THE BLIND SPOT

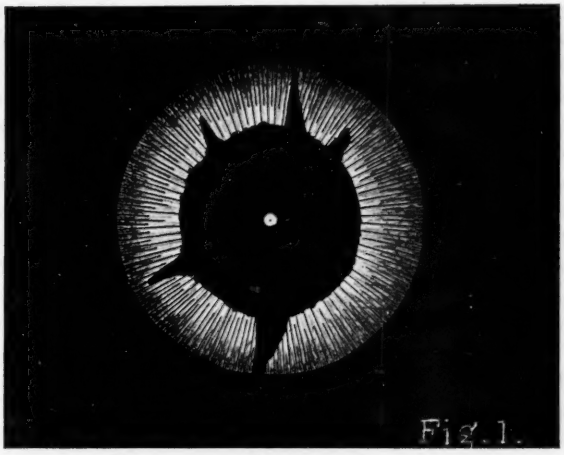
(1) The blind spot is an old battle-ground of the physiologists and psychologists, and although the author cannot claim that his conclusions are altogether new, the subject of the "filling-in" of the blind spot is still one of controversy. It is the author's belief that the evidence he offers and the arguments he puts forward should go a long way towards finally settling the question.

He claims to show beyond dispute that this filling-in can only be accounted for on the basis of *suggestion*, that is to say the solution is psychological rather than physiological.

As illustrating the diversity of view that exists on this subject a lengthy paper by H. Helson, published as recently as 1929[1], purports to prove that the blind spot is not really blind but will respond to direct stimulation, and he argues at length that it is possible on the basis of his observations to account for the filling-in of the blind spot. It seems to the author that if, as alleged, the blind spot will respond to direct (light) stimulation, the conditions under which this can take place are so far removed from the ordinary conditions of observation that the phenomenon can have no bearing whatever on the point at issue. As a crucial test of Helson's contention the author has made observations with the eye in a state of partial dark adaptation on lights of great intensity. For example, a powerful electric torch was set up at a distance of 25 ft. The background was a brick wall with white pointing, and the general illumination (twilight) was just sufficient to enable this to provide convenient points for fixation. The author found that when the fixation point was properly chosen there was no trace whatever of any central point of light in spite of the brilliance of the source. There was observed a glare, which, when the gaze was held steady, faded after some 6 or 8 sec., after which no light whatever could be sensed. By moving the direction of vision about 1 degree more or less to the right or left the glare reappeared, but now unsymmetrically with a bias to the

[1] *The American Journal of Psychology*, vol. XLI, July 1929.

left or right of the blind area. The glare is evidently due to the corona[1] which surrounds the retinal image of every bright light and subtends an angle of from 8 to 10 degrees. The blind spot which subtends an angle of only 5 degrees can mask only the central part of the corona, the outer part of which falls on the retina and so gives rise to the glare; after a short lapse of time fatigue sets in and the glare is no longer sensed. The relation of the corona to the blind spot is illustrated by fig. 1, in which the blind spot shown is a plotting from that of the author's left eye. During the whole period of observation there was no sensation received from the direct image; the beam from the electric torch focused on the blind spot failed to excite the least response. Moreover, to test the possibility of this being due to rapid fatigue the author made



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excursions with the fixation point so that the position of the image on the optic disc must have been changing correspondingly, yet there was no trace of response to the direct image, although the glare could be renewed after fading by this means. Another test was to shade the half of the retina including the blind spot but leaving the fixation point visible; when the shade was suddenly withdrawn the glare appeared, but still no trace of the direct image.

[1] The *corona* of which mention is made in the present paper is a quite familiar phenomenon. It is the main cause of the glare or dazzle produced by a motor head-lamp or other bright light. It is probably caused by diffraction due to the cellular structure of the cornea and crystalline lens. With a brilliant light source the corona to all intents and purposes masks or "blanks-out" all objects in the field of vision within a contained angle of some 8 or 10 degrees. It is a curious fact that although the corona is a perfectly well-known phenomenon and obvious to the most ordinary or casual observer the author has searched most of the books on the subject without finding the barest mention or allusion to the subject.

The halos typical of glaucoma and other pathological conditions may be regarded as abnormal manifestations of the corona.

Nevertheless, the account given by Helson cannot be dismissed altogether as a fantasy; it would appear that he took every precaution to ensure rigid conditions of observation, and he devised much special apparatus and employed trained and selective observers. One can only suspect that in devising so elaborate a scheme of "control" the conditions became foreign to those of common observation.

In all differences of opinion where subjective observations are concerned individual peculiarities may play an important part. For example, many observers claim that they are able to *see* their blind spot as a dark patch when looking at a light-tinted uniform ground. The author has tried and tried again times out of number to confirm this, and not once has he been able to distinguish anything of the kind.

Some six years earlier than Helson a paper was read by K. Koffka[1] which also reported the blind spot as responding to direct stimulation, but in this case the experiments related to real and apparent movements of a light source or sources, and were capable of more than one interpretation.

But the author contends that all this is beside the point; we can leave the question of the light sensitivity of the disc or blind spot to be fought out between those who claim to give proof by refined and super-controlled observation and the histologist who will look for positive confirmation in the form of some light-receptive end-organ extending or distributed over the area of the disc. Any suggestion that the nerve fibres themselves are responsible may be ruled out at once, since the sensation in such case would be attributed to the regions served by the nerve fibres in question. And since Helson reports not merely the sensation of luminosity but further the appreciation of *form* in the area constituting the blind spot, the said area (if his observations are correct) must be served by sensory nerve elements in orderly arrangement.

Before leaving the subject and embarking on a description of his own observations, the author thinks it well to state that he has been unable to confirm Helson's results: he is at least satisfied that his own blind spot is in fact blind.

(2) The blind spot of the retina, where the optic nerve enters the eye and which is normally situated some 15 or 16 degrees from the fovea centralis or macula (on the nasal side), does not and cannot itself be a means of conveying sensation to the corresponding (opposite) occipital cortex, at least this is generally agreed by physiologists. Nevertheless, the field of vision shows no fault or vacancy, the "picture" appears complete.

With binocular vision this is to be expected, since the blind spots in the two eyes are on opposite sides, and though leaving blanks or vacancies in their respective (opposite right and left) fields the combined cortical image is complete. But, with one eye only in use, still the blind spot does not appear as a vacancy, that is to say it does not give an impression of absence of light, i.e. blackness. If we view a black spot on a white ground the ground appears

[1] Seventh International Congress of Psychology, July 1923.

unbroken; uniformly white. If it be a white spot on a black ground the ground appears uniformly black. Hence there seems *prima facie* evidence that the *lacuna* caused by the blind spot is filled by *borrowing*. Some years ago the author, starting on the above assumption, endeavoured to ascertain the particular nature of this *borrowing* and the laws controlling it; the results were entirely negative. Recently this interrupted investigation has been resumed and the previous conclusion confirmed, namely, that it is impossible to account for the filling-in of the blind spot on any theory based on borrowing.

By a process of elimination the possibility of accounting for the filling-in of the blind spot by the physical or biophysical borrowing of light (white or colour) from the surrounding parts of the retina, is shown to be untenable. Thus it is proved (*a*) that there is no distortion such as would denote geometrical borrowing; (*b*) there is no evidence of borrowing or filling-in with the predominant tone or colour; (*c*) there is no evidence of average-tone or mean-tone borrowing; (*d*) there is no bias in favour of black or white or other colour; (*e*) there is no preference shown or predominance in any particular direction, i.e. horizontally or vertically in the tone assumed.

But there *is* evidence that the vacancy or lacuna created by the blind spot is filled by *suggestion*, that is to say, the impression formed in the cortex (counterpart to the image on the retina) is referred to some higher nerve centre to have the deficiency made good, and then passed to the final sensory centre wherever that may be. We may think of this just as a damaged or unfinished picture might be submitted to a restorer or an artist to make good or to complete.

(3) *The Evidence.* (i) The possibility we will consider first is that of the lacuna being filled in by a *distortion* of the surrounding field in which a lattice of Cartesian co-ordinates takes on what we may term Gaussian characteristics (figs. 2 *a* and 2 *b*). To establish this the visual impression when centring the blind spot in fig. 2 *a* should be of the type shown in fig. 2 *b*. Nothing of the kind is observed; the "chess-board" surrounding the blind spot shows no trace of distortion. The same may be observed in figs. 3 *a* (and 3 *b*), when the central "bull's eye" is made to vanish the members of the lattice framework remain unaffected.

N.B. Figures having the suffix *a* are black on white, those with the suffix *b* are white on black. For publication it has not been thought necessary to reproduce figures with the *b* suffix, i.e. black ground.

(ii) The blind spot as affected by the majority or predominant tone. In figs. 4 *a* (and 4 *b*) the blind spot is made to occult the break on the broad band of black on white or white on black as the case may be. It will be observed that when the break is no longer visible the band becomes apparently continuous, showing that contrary to expectation the lacuna is filled by the tone which locally and generally is in a minority. This figure may be used in different positions in order to ascertain whether there is any difference or bias in favour of the horizontal or vertical direction, such as to suggest that borrowing

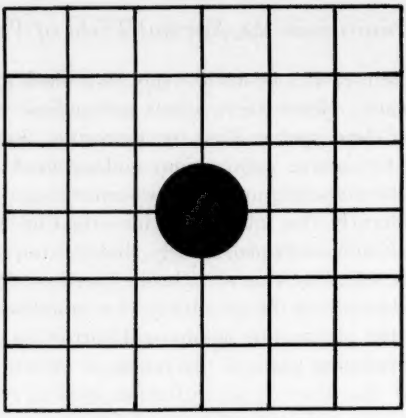


Fig. 2*a*. (Half original size.)

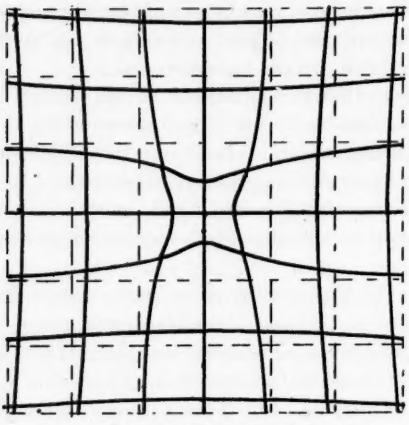


Fig. 2*b*. (Half original size.)

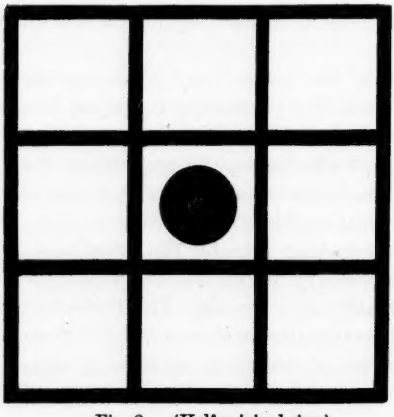


Fig. 3*a*. (Half original size.)

might take place more freely above and below than from side to side or *vice versa*. Observation gives a negative reply.

Figs. 5 *a* (and 5 *b*) are similar to those last discussed, but the band is narrower and the gap wider. Similar observations on these figures give identical results, but now any possibility of borrowing becomes more remote, for on fig. 5 *a* the white ground is overwhelmingly preponderant yet the black line bridges the lacuna. Similarly in fig. 5 *b* the black preponderates but the white line holds its own. It is most interesting to vary the distance of these figures from the eye whilst gazing intently on the c.v. The gap in the line is clearly visible until occulted by the blind spot, then the line is seen to bridge the gap

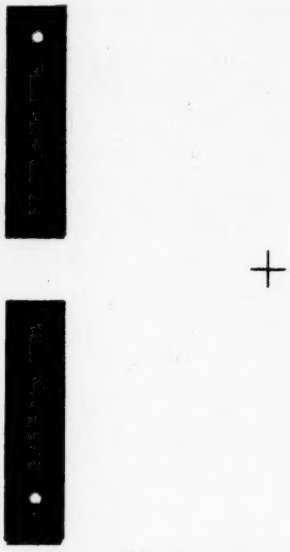


Fig. 4*a*.

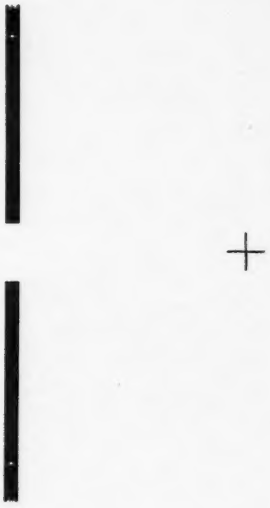


Fig. 5*a*.

as though the two ends were stretching out to meet each other like fingers; then, as the figure is moved beyond the critical distance, the "fingers" recede and the gap is re-established.

The teaching of figs. 4 *a* (and 4 *b*) and 5 *a* (and 5 *b*) is conclusive also as to directional borrowing. Looking at these figures with the lines or bands vertical we could believe that borrowing was taking place vertically from above and below. But when the figures are turned through a right angle so that the lines or bands become horizontal the observation is unaffected and we should have to assume that the borrowing took place from right to left. So that there is no question, directional borrowing cannot be the solution.

All observations made with these figures are symmetrical as concerns

black and white, there is no preference shown by the *lacuna* for the one or the other.

(4) It appears to the author that all the possibilities of purely physical or biophysical explanation of the phenomenon have been exhausted with completely negative results. The fact emerges that the sensory lacuna created by the blind spot is filled in as an "intelligent anticipation" of what ought to be there having regard to the context. Thus the two parts of a straight line entering and leaving the lacuna suggest continuity, and forthwith we see continuity. The experiment described, in which the figure is moved towards and from the observer, is particularly interesting in this respect, because in spite of seeing the gap and knowing it to exist one moment, the next instant it is gone and the line is uncompromisingly continuous; definite knowledge and volition will not overcome the "illusion" any more than we are able when looking at a straight line in the ordinary way to create a visible gap by force of will.

The implication of this, namely, that the cortical picture is submitted to a higher centre, where it is "touched up" before it is allowed to be "sensed," might be deemed too improbable to find acceptance, but a little consideration will, the author thinks, dispel this feeling; there is abundant evidence that this is a general truth, not merely as concerns the blind spot, but broadly as concerns the neurology of vision. For example, the artist whether in black-and-white or colour, more especially the impressionist, bases his work largely on suggestion; we see people and other familiar objects on his canvas which when examined closely turn out to be nothing but a few disconnected lines or patches of colour, and we are surprised at having been "taken in."

The blind spot itself is only approximately circular; it may be shown that it has tentacula which correspond to branches from the optic artery. Thus in fig. 1, plotted from the author's left eye[1], looking at the c.v. mark at a distance of about 18 in., the disc (and branches) entirely disappears. This figure is one subject to individual variation. It is important therefore that when preparing a figure for test purposes, such as figs. 5 *a* (or 5 *b*), either the lines should be of sufficient breadth to remain unaffected by these tentacles, or the position of the latter should be taken into consideration when using the figure.

(5) Previous observations are said to have been made on somewhat similar lines to those described in this paper, but the author has been unable to find any clear parallel. Both Helmholtz and Aubert have been cited, but the originals are very inaccessible. There is nothing in Sterling's work or Gray's *Anatomy*, except the mention of the blind spot and the usual conventional diagram. Likewise in Prof. Luciani's *Human Physiology* there is nothing relevant. In Edmund Sanford's *A Course in Experimental Psychology* (pp. 102–4) a diagram is given, reproduced here as fig. 6. Referring to this the text has it, "When the image of the middle of the diagram falls upon the blind spot one

[1] This plotting of the blind spot with its tentacula in this manner is not new.

bar will seem to cross completely over the other. Bars that cross are so much more frequent in experience than those that are mitred together that the sensations of the adjacent parts are thus interpreted." The author (Sanford) goes on to say that: "Both Helmholtz and Aubert find themselves unable to determine how the parts of the figure resting on the blind spot are related." So it would appear that the diagram figured has been discussed by these authorities.

Fig. 6. (Half original size.)

In the author's view the diagram in question most perversely misses the mark. It seems designed to confuse the interpretation just as would any other complicated pattern. The "Picture restorer" who is responsible for filling in the blind spot is quite childlike, he requires a very clear indication or hint before he will respond with decision.

Summary

In demonstrating the "blind spot" it is customary to exhibit either a black spot on a white ground or a white spot on a black ground; in either case the visual impression is that the spot vanishes, i.e. assumes the tone of the background. From this it has been inferred that the blind area is "filled-in" by borrowing from the surrounding field. The present paper describes experiments conducted by the aid of specially designed diagrams by means of which it is claimed to prove:

(1) That geometrical borrowing does not take place.

(2) That the filling-in cannot be accounted for by the borrowing of tone or colour from the surrounding field.

(3) That the filling-in of the lacuna takes place in some nerve centre or in some part of the cerebral cortex by a process akin to *suggestion*.

PART II. ON A BLIND OR INSENSITIVE HIATUS OR RIFT IN THE FIELD OF VISION

(1) When engaged in making observations on the blind spot as described in Part I of the present paper the author located a blind or insensitive area constituting a vertical rift or hiatus, the site of which appears to be the junction between the right- and left-hand retinal areas, extending upwards and downwards from the macula. The macula itself is not involved.

So far as the author has been able to ascertain, the existence of this vertical hiatus or rift in the visual field has not previously been observed or even suspected. It may or may not be capable of being identified in the retina itself, it might have its origin elsewhere.

In view of the fact that the nerves from the right and left halves of the retinae separate and are connected (indirectly) with the right- and left-hand cortices respectively, it might be expected that the junctions would show some visual imperfection or irregularity of which it would be difficult to predict the nature. A perfect join without overlap or other failure to register correctly, in every human subject, in health or disease, does not seem probable; yet if there is a hiatus or lacuna in the boundary region, as the author claims to have proved, the questions arise: How is it filled in, and why so difficult to locate?

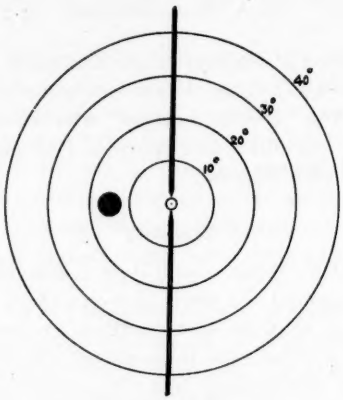


Fig. 7.

(2) The author's observations would indicate that the right- and left-hand visual fields of the retina are associated in the manner indicated in fig. 7, namely, they overlap (this is usually accepted[1]) in the region of the macula, and do not quite meet above and below, leaving between them a hiatus or insensitive rift. The width of this rift is in the region of 10–20 min. of arc.

(3) *The Observations.* (See also diagrams 1–5 on fig. 11.) Fig. 8. Fixing the eye (either right or left) on the + mark the diagram is slowly tilted right to left, first one way and then the other, passing through the vertical; when the two observation dots are vertically over the + mark they may be observed to vanish, with some observers simultaneously, with others successively. Until the observer has had some practice in making these observations he may notice that the dots become indistinct and perhaps momentarily fade and then return, or he may report some change in their appearance, but he finds

[1] Not by all authorities.

it difficult to make them completely vanish. This is due to the fact that it is not easy to keep the eye fixed firmly on the + mark; as soon as either of the dots becomes indistinct the eye involuntarily goes in search of it, and it is, to some, most difficult to overcome this reflex.

Fig. 9. Here there are three dots at equal distance from the + mark; the upper one is the observation dot, those to the right and left are control dots. In view of the fact that it commonly takes some 2 or 3 sec. (even with practice) to make an observation successfully, it seemed to the author that optical *fatigue* might be playing a part in the vanishing of the dots, and fig. 9 was designed to put this to the test. The figure is slowly rotated to-and-fro about the + mark as centre, so that the observation dot and the two control dots make journeys on the retina equal in space and time. The observation dot will be found to vanish while the two control dots remain

Fig. 8. (Half original size.)

Fig. 9. (Half original size.)

clearly visible. This is put forward as a proof that the disappearance of the observation dot is not due to fatigue; or, in order to be on the safe side, this conclusion may be expressed in less positive terms—the disappearance of the observation dot is due, in part at least, to some considerations other than normal fatigue.

Fig. 10 consists in a black circle on a white ground, at whose centre the + mark is situated. There are three gaps in the black line or band, one observation gap vertically over the + mark and two control gaps, one to the right and one to the left. The figure is employed in the same manner as fig. 9; the upper or observation gap is seen to close up, whilst the two control gaps remain clearly visible. This figure goes further than fig. 9. It will be observed that when the observation gap closes there seems to be perfect continuity of the black line, and in this respect the observation is comparable

with those made in connection with the investigation of the blind spot; it is consistent with the view that the insensitive hiatus is filled by *suggestion*.

By appropriate test cards the alignment of the rift in the upper and lower fields of vision can be demonstrated, i.e. above and below the macula; many observers have found that all four observation dots may be made to vanish simultaneously.

Any of the diagrams may be used with binocular vision to prove whether the rifts in the two eyes coincide; it appears that with most observers they do so, which means that their positions in relation to the macula are identical. Diagram 4, fig. 11, is the most spectacular for this purpose; it is quite impressive to see the whole four dots vanish entirely.

Fig. 10. (Half original size.)

Young people are best adapted for making these observations, but so long as ordinary press matter from a daily paper can be read easily at a distance of 2 ft. with one eye closed no more drastic eyesight test is necessary.

(4) The author's observations are supported by the evidence of six independent observers whose reports form an appendix to the present paper.

The author's view at the time of going to press is that the hiatus is a region *very quickly* fatigued rather than totally blind.

Note. It has been suggested to the author that the disappearance of the dots might be explained by their being occulted by blood vessels and that it is therefore not necessary to postulate a blind "rift" to account for the observed facts. The answer to this is, in that case the positions at which the dots should vanish would not always be on the vertical line, but distributed elsewhere. Beyond this, with a little patience a vertical line of some length may be made wholly to vanish.

Summary

The author sets out to demonstrate the existence of a blind or insensitive "rift" or "hiatus" consisting in a narrow vertical region extending from above and below the macula into the outer field of vision, presumably coincident with the line of demarcation between the right- and left-hand halves of the retinae as related to their cortical projection. The breadth of the "hiatus"

is found to be in the neighbourhood of ten or twenty minutes of arc, and it approaches the *fovea* from above and below to within about 1 to 2 degrees.

The "rift" or "hiatus" is demonstrated by the aid of a number of specially prepared diagrams, and the facts of observation have been confirmed by six independent observers (students of the Birmingham University Department of Anatomy). The exact nature of the lack of sensitivity has not been determined; it is not known whether it is a definitely blind area or whether it is virtually blind by reason of its being quite abnormal in its susceptibility to fatigue[1]. As in the case of the blind spot there is evidence to show that it is filled by suggestion.

ACCOUNT OF TESTS CONDUCTED IN THE DEPARTMENT OF ANATOMY OF THE BIRMINGHAM UNIVERSITY
23 March, 1933

Five diagrams were made use of, Nos. 1, 2, 3, 4 and 5, fig. 11. Drawings of these to a reduced size ($\frac{1}{4}$ full scale) are attached. The observers were six in number, pupils of Professor Lockhart.

The only instructions given in the first instance were those reproduced on p. 237. In accordance with these instructions the first observations were made with no hint or suggestion of what was to be looked for or expected. After these observations had been made and recorded by the observer without any assistance from the author whatever, the observer was instructed to draw a line across the report, and the object of the further observation was explained to him (or her). Further observations were then made on diagrams, more particularly Nos. 2, 3 and 4. In some cases diagram 5 was used.

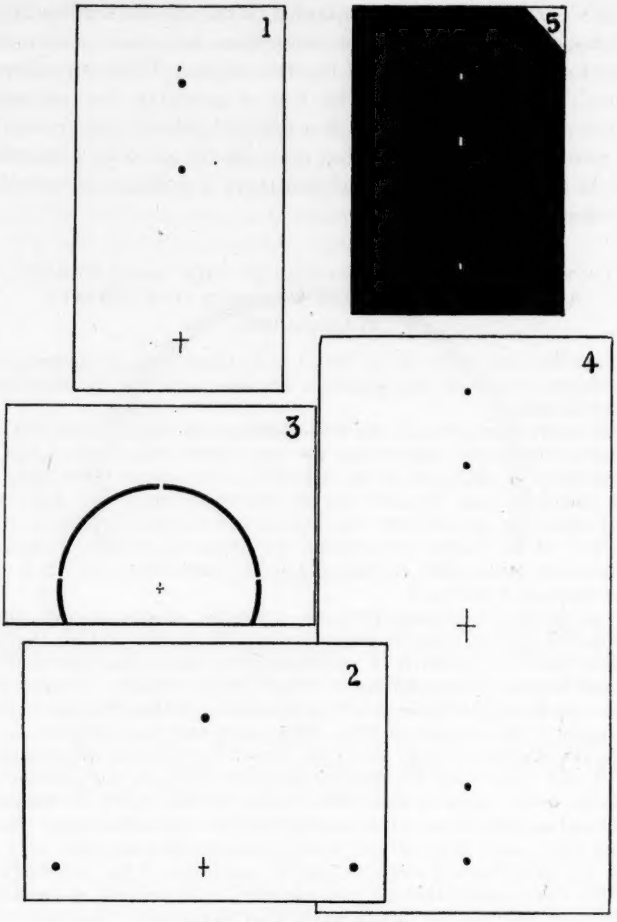
After one or two preliminary trials the procedure adopted was as follows: The observer, seated on the opposite side of the table to the author, having made acquaintance with the contents of the instruction sheet, was examined as to his eyesight, and diagram 1 was exhibited starting with an inclination of about 20 degrees to the right and it was slowly moved to an inclination of about 20 degrees to the left, and back again to the original position. This movement was executed as smoothly as possible, the observer, usually about the second or third time the diagram passed the vertical, said "stop" and the diagram was held steadily in the position called for. Sometimes he would begin to make notes before having called for the diagram to be stopped and on other occasions he would begin his notes afterwards. The diagram would from the time he said "stop" be moved as he might indicate.

It was only after the test as above and the conclusion of the observer's notes relating to his observations that he was informed of the purpose of the test. A line was then drawn and all observations made after the observer had been enlightened as to the object of the tests were entered below this line.

The diagrams, fig. 11, are drawn to quarter scale. Diagram 1 consists of two dots 2 in. apart vertically over a cross, the latter being the centre of vision. The first portion of each report relates to observations on this diagram. Diagram 2 consists of three dots equidistant from a + denoting the centre of vision. One dot is vertically over the centre of vision, the two other dots are to the right and left. The function of this diagram is to prove that the disappearance of the vertically situated dot is not due to normal fatigue. All observers agreed that the dot over the centre of vision disappeared, whilst the two control dots remained clearly visible. The manner in which

[1] Most probably so.

the diagram was used consisted in rotating it slowly about the centre of vision so that all three dots made paths on the retina equal in space and time.



Diagrams 1–5. ($\frac{1}{4}$ full scale.)

Fig. 11.

Diagram 3 resembles diagram 2 in its purpose, but instead of the dots there are breaks in a circular black band, and when the break vertically over the centre of vision is occulted the band appears to be continuous, which supports the view that the line streak or fissure is filled in the same manner as the blind spot by "suggestion."

Diagram 4 is a double edition of diagram 1, from which it may be shown that the blind fissure is, with many people at least, almost perfectly straight. In using this diagram the discovery was made that the observation of the blind fissure can be

carried out with binocular vision. When this diagram is set up (full size) 4 or 5 ft. distant, many observers with both eyes open are able to find a position; when gazing steadily at the centre of vision all four dots disappear.

Diagram 5 is similar to diagram 1, but with white dots on black ground.

INSTRUCTION SHEET, 23 March, 1933

Look steadily at + with one eye closed or shielded and report any change in the appearance of the two dots (in the diagram vertically over centre of vision) whilst the diagram is moved from a position sloping in the one direction to a position sloping in the opposite direction, and make a note or report of any change in the appearance of the two dots seen in the outer field of vision.

N.B. Eye must not be allowed to wander from the mark.

Alternative. Lean diagram against a book or other support and incline head from one side to the other instead of inclining the diagram.

Make notes of your observations on sheet provided as they occur to you.

Observer. J. H. A.

No. 1. Disappearance of lower spot when paper held vertically. Disappearance of both spots when paper held vertically. They return successively as the paper is inclined, the upper first.

Paper stationary, head inclined. Both spots invisible when head vertical; when inclined the spots return successively, the upper one first.

No leading questions were asked.

No. 2. Top spot disappears, two lateral ones are visible.

No. 3. The superior gash in the circle closes when the cross is fixated with the head held vertically, though the two lateral ones are still visible.

No. 4. *Left eye:* Head vertical. Cross fixated. Upper and lower pairs of spots disappear. *Both eyes:* Head vertical. Cross fixated. Upper and lower pairs of spots disappear, but return on inclining the head.

Observer. (*Miss*) *B. B. B.*

The spots disappear at the vertical position (not sure whether both spots, or only the lower one disappear).

The above observation was made without any leading question.

Diagram 2. Upper spot disappears—the other two quite plain.

Diagram 3 (not successful).

Diagram 4. Upper two spots disappear completely, lower two visible.

Diagram 5 (black). Both spots disappear.

Observer. I. D. Egypt (*Cairo*)

In the middle and towards the right side one lower spot disappears.

The lower and upper spots disappeared when the board was moved to the right.

Diagram upside down. The lower point did not disappear. The point above disappeared as the board was moving from right to left.

The above notes are made without any assistance and they represent my own observations.

Diagram 5 (white on black). The two spots disappeared as the board moved to the right.

Diagram 2. The upper spot disappeared but the control spots do not disappear.

Observer. P. N. C.

Diagram 1. *Vertical:* First the top can only be seen, nearly vertical. Second disappears. *Inverted vertical:* can see dots but only very faintly. Second observation showed the middle dot to disappear.

No assistance was given.

Diagram 2. The top spot disappears in vertical position, the two lateral spots always clearly visible.

Diagram 3. Control gaps remain but in vertical position the top gap disappears.

Diagram 4. *Binocular.* The dots definitely go faint but do not completely disappear.

Observer. (Miss) E. C.

Diagram 1. Spots get nearer as paper placed vertically. Whichever way paper being rotated. Lower spot becomes fainter, when paper leaned to right lower spot appears to move left. Upper also moves but less. Lower spot almost disappears when paper made vertical. *Upside down:* Upper spot becomes fainter.

Above observations have had no help.

Diagram 2. Rotated about centre of vision. When top spot disappears the others still remain.

Diagram 5 (white on black ground). White spots disappeared, the lower one first. *Upside down:* Lower spot went first. Then both disappeared (when paper vertical).

Diagram 4. All spots went when head vertical (possibly slightly to left).

Observer. G. M. G.

Diagram 1. As the diagram is moved towards the middle line the two dots appear to elongate and then disappear when the dots are in the middle line.

This observation was made without any external assistance.

Diagram 2 (inverted). As the paper is rotated around cross dot No. (3) disappears while dots Nos. (1) and (2) remain visible.

SOME OBSERVATIONS ON THE DEVELOPMENT OF THE VAGINA IN THE PIG

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A CONSIDERABLE amount of evidence has now been brought forward to show that developmentally the vagina is a compound organ, in at least several mammalian forms. Further, this evidence indicates that the mode of development of the vagina differs very considerably in different orders and even among the members of one order of Mammalia, and it appears certain that the descriptions which seek to establish a uniform developmental process, differing only in details, for the vagina in the mammals above the marsupials can now no longer be accepted.

In a recent paper (1) I have brought forward evidence to show that the variations in the developmental process are closely correlated in the rodents with the anatomical differences of the lower part of the female genito-urinary tract. A study of the development of the vagina in the rabbit showed that the upper portion was derived from the Müllerian ducts, while the lower and lesser portion arose from the fusion of two Wolffian bulbs with one another. In the rabbit the vagina communicates with the exterior through a fairly long urogenital sinus. In the rat (Mijsberg (2)) the same structures, Müllerian ducts and Wolffian ducts, are concerned in the formation of the vagina, and, in addition, the urogenital sinus divides into two canals and the dorsal canal forms the lowest part of the vagina. In the rat the vagina opens directly to the exterior, the genital tract being thus more completely emancipated from the urinary tract than in the rabbit; and this emancipation is to be associated with the additional developmental process at the lower end.

The developmental processes of the rabbit and the rat suggest the nature of the compound formation of the vagina, but before a complete understanding of the morphology of the vagina becomes possible, descriptions of the developmental processes in other mammalian orders are required and their correlation with the varying anatomical forms must be established. The Ungulata have not yet been extensively studied. The descriptions of the development of the vagina in this order are not very complete and in several points they are contradictory. I have studied the developmental processes in the pig as part of the wider investigation of the development and morphology of the vagina in the Mammalia on which I am at present engaged. In this paper I present the description of the development of one form as a necessary preliminary to the consideration of the vagina in the Ungulata generally.

Felix and Bühler (3) give the same description for ungulates as they do for other mammals, namely, that in all the vagina is formed solely from the fused Müllerian ducts. Henneberg (4) has described the formation of the external genitals in the female pig, and he notes in his account that the urogenital sinus is split into two parts (dorsal and ventral) from above downwards by a frontal division. The anterior channel becomes the urethra, the posterior one aids in the building of the vagina. In a female foetal pig of 12 cm. C.R. length Wood-Jones (5) has described the fusion of the lower ends of the Müllerian ducts with the Wolffian ducts and the entry of the latter ducts into the urogenital sinus. He has interpreted this as a stage in development where there exists a median Wolffian chamber into which the Müllerian ducts will open later in foetal life. Tourneux (6) gives an account of the vaginal anlage in a foetal horse, and shows that in its lower part the Müllerian and Wolffian ducts blend to form a common canal. On the other hand, Retterer (7) found that the lower part of the vagina in the horse and the calf was split off from the upper part of the urogenital sinus by the formation of a frontal septum. Bergschicker (quoted by Mijsberg) studied the Müllerian and Wolffian ducts in the cow and found that the Müllerian ducts fused with the urogenital sinus for some distance at their lower ends. The Wolffian ducts thus obtained a definitive opening into the lower part of the vagina.

THE PIG

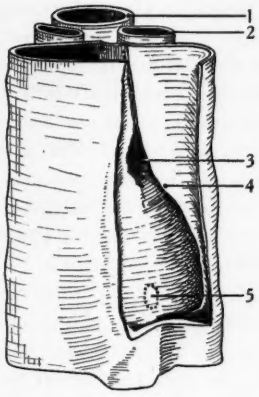
The Müllerian ducts in the pig fuse with one another in the genital cord to form the utero-vaginal canal in the same manner as in other mammals. According to Tourneux and Legay (8) the fusion occurs when the foetus measures about 60 mm. from vertex to rump and commences towards the middle of the genital cord. My material does not show the place of first fusion of the Müllerian ducts, but it does indicate clearly that the lower ends of the Müllerian ducts remain separate until quite late in foetal life (see text-fig. 2).

Shortly after its formation (8·2 cm. stage) the vaginal anlage consists of an epithelial tube, oval in transverse section, which bifurcates at its lower end; and each limb of the tube comes into separate contact with the dorsal wall of the urogenital sinus. The wall of this tube and of the limbs consists of a single layer of columnar epithelial cells, but the extreme lower ends of the separated extremities are solid, each end being filled up with a mass of polyhedral cells. This solid portion of each duct corresponds with the part in contact with the urogenital sinus[1].

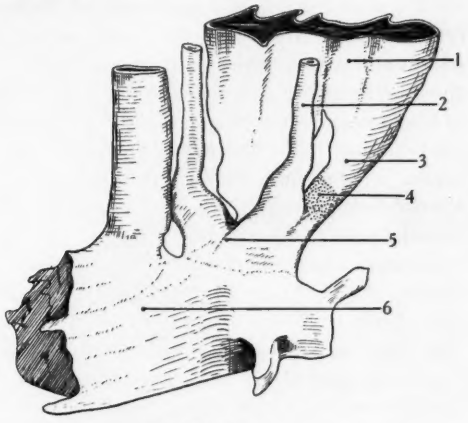
The Wolffian ducts appear to open into the urogenital sinus cephalad to the level of contact of the Müllerian ducts with the sinus. At first sight this relationship between the ducts seems distinctly unusual, but closer examination

[1] The presence of a distinct basement membrane on the dorsal wall of the sinus, between it and the tips of the Müllerian ducts, would make it seem very unlikely that an upward proliferation of sinus epithelium into the lower ends of the ducts ("conus vaginalis" of Spuler) had occurred. These cells are almost certainly Müllerian in origin and have been formed *in situ* by proliferation from the growing tip of the duct.

suggests, I think, the interpretation. Inspection of the dorsal wall of the urogenital sinus in a wax-plate reconstruction of this stage (text-fig. 1) indicates that the terminal part of the Wolffian duct has the form of an elongated funnel. (This is confirmed by the study of a graphically reconstructed paramedian section through the ducts and sinus (text-fig. 5 A).) There is an inwardly projecting ridge on each side on the inner wall of the sinus. When traced upwards this ridge is found to be continuous with the upper margin of the apparent opening of the Wolffian duct; followed downwards it runs upon the lateral wall of the sinus to the level of the termination of the Müllerian duct, and



Text-fig. 1.



Text-fig. 2.

Text-fig. 1. Drawing of a wax-plate reconstruction of the lower end of the genital cord of an 8·2 cm. female foetal pig. The reconstruction is viewed from in front and slightly from above. The left half of the anterior wall of the urogenital sinus has been removed: (1) fused Müllerian ducts; (2) Wolffian duct; (3) opening of left Wolffian duct into sinus recess; (4) overhanging edge of this opening continuous with fold on lateral wall of sinus; (5) point of contact of Müllerian duct with sinus.

Text-fig. 2. Drawing of a wax-plate reconstruction of the lower end of the genital cord in a female foetal pig of 12·4 cm. C.R. length. Only the epithelial structures are represented, and the reconstruction is viewed from in front and from the left side: (1) fused Müllerian ducts; (2) Wolffian duct; (3) Müllerian vaginal cord; (4) upgrowth of Wolffian epithelium on anterior aspect of left vaginal cord; (5) median canal; (6) urogenital sinus.

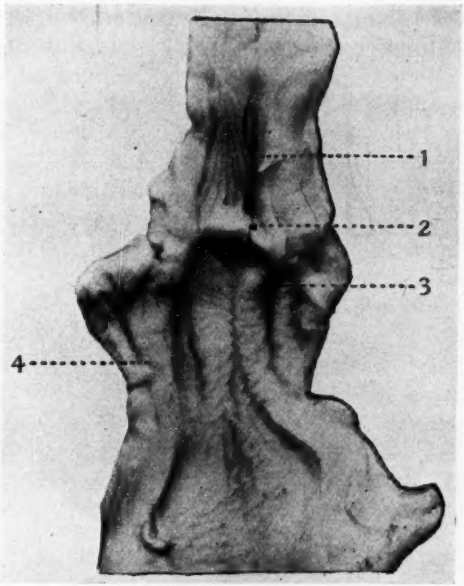
there it turns fairly sharply medialwards and disappears. A transverse section of this part of the sinus (Plate I, fig. 1) shows that the two ridges are the anterior boundaries of dorso-lateral bays, each bay being perfectly continuous in an upward direction with the lumen of the corresponding Wolffian duct. The epithelium lining the sinus and the bays is stratified, the cells being polymorphous. It is lower in the bays (about three cells thick) than elsewhere on the sinus walls, where it averages five to six cells in thickness, but there are no *definite* cytological differences to be detected between the epithelia of the dorsal and ventral walls of the sinus.

The tubular vaginal anlage now grows and enlarges both in length and breadth. Longitudinal ridges begin to be evident upon the inner surface of the hollow portion, especially towards the lower end (12·4 cm. stage). The lining epithelium of this part is still seen, in sections perpendicular to the free surface, to consist of a single layer of columnar cells. Traced downwards the vaginal anlage bifurcates, each separate part being formed by a solid cord of epithelial cells and representing the terminal non-fused part of a Müllerian duct (Plate I, fig. 2). The corresponding Wolffian duct lies anterior, and somewhat lateral, to the Müllerian cord. As these structures are traced caudally Wolffian cells are found on the anterior aspect of each Müllerian cord (Plate I, fig. 3). These cells are in the form of a solid mass which, when traced caudally, becomes patent and soon establishes an open connection with the Wolffian duct proper, the duct itself being now definitely enlarged (see text-fig. 5 B for the relations of Wolffian and Müllerian epithelium at this stage). At a lower level the Wolffian ducts fuse with one another in the middle line, the lumina however remaining separate for a short distance (Plate I, fig. 4). The Müllerian epithelium has almost disappeared at this level, being represented only by a few cells on the dorsal aspect of the left duct. A short distance further caudally the Müllerian epithelium has completely disappeared and the Wolffian ducts form a single median canal. The wall of this canal consists of a stratified epithelium, the constituent cells of which are characterised by the clearness of the cytoplasm. The canal continues for some distance further caudally and then opens into the dorsal part of the urogenital sinus (Plate I, fig. 5). In the sections at this level the cells of the Wolffian canal quite markedly differ from the cells of the sinus in the better staining of the cytoplasm of the sinus cells with Orange G.

In a foetus of 17·5 cm. C.R. length the solid Müllerian epithelial cords have commenced to fuse in the middle line and they have become relatively shorter. There is as yet no communication between the upper tubular (Müllerian) part of the vagina and the median (Wolffian) canal below (Plate I, fig. 6). The Wolffian ducts open into the Wolffian canal a short distance below the junction of the solid Müllerian cords with it. Above its solid ends the Müllerian vaginal anlage is lined with a single layer of columnar cells; and with the further growth the longitudinal folds of the epithelium in its upper part have become more numerous.

At a slightly later stage (18·2 cm. C.R. length) the upper part of the vagina is still lined with a single layer of columnar epithelial cells. The Wolffian ducts lie anterior to this part of the vagina, one on each side of the middle line, and are clothed with a cubical epithelium. As the sections are followed caudally small isolated areas which show the first appearances of stratification of the epithelium are found in the vaginal mucosa. Further caudally these areas become larger and more numerous, and they are finally continuous, so that for some distance above the terminal solid epithelial cord the vagina possesses a stratified epithelial lining, two or three cells thick. This part of the vagina terminates in a very short epithelial cord, evidently the result of fusion of the

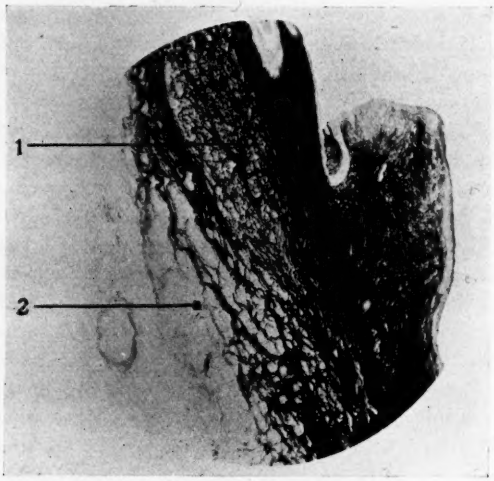
paired cords of earlier stages. The lower end of this Müllerian cord shows a sudden transition in cell type to the form which was previously recognised as Wolffian in the mass of cells which connected the Müllerian epithelial cords with the sinus at the 12·4 cm. stage. This Wolffian cord divides into two when traced further caudally, each part becomes progressively larger, acquires a lumen and finally re-unites with its fellow and with the corresponding Wolffian duct. The united structure passes on as the median Wolffian canal and terminates in the sinus.



Text-fig. 3. Photograph of the vagina and urogenital sinus of a 35 cm. sow laid open from the ventral aspect, ×3. (1) Müllerian vagina; (2) "hymen"; (3) opening of Gärtner's duct; (4) opening of urethra into urogenital sinus.

A young sow (6 weeks old) measuring 35 cm. from vertex to rump afforded me an opportunity to study the vagina with particular reference to the presence or absence of "hymeneal" structures. According to Weber(9) there is a circular constriction where the vagina joins the urogenital canal in many ungulates, and this constriction may be supplemented by transverse folds of the mucous membrane. On laying open the vagina and urogenital sinus of this specimen from the ventral aspect, the appearance figured in text-fig. 3 was found. There is clearly seen to be a circular fold of mucous membrane constricting the vagina and separating off an upper part from the remainder. This upper portion shows numerous delicate longitudinal ridges and furrows,

and quite definitely corresponds with the upper tubular part of the vaginal anlage of early stages. A short distance below the circular fold there is seen on each side the opening of Gärtner's duct, and below this level is the opening of the urethra into the urogenital sinus. A few longitudinal ridges of mucous membrane run downwards from the openings of Gärtner's ducts, but this part of the vagina is relatively smooth walled. The "hymeneal" fold lies therefore between the Müllerian vagina above and the median Wolffian canal below, and in this position it does not guard the opening of the vagina into the sinus. A vertical section through the "hymeneal" fold is shown in text-fig. 4. It has the form of a transverse shelf in the vagina, more apparent from the upper aspect. Both surfaces of this shelf are clothed with stratified squamous



Text-fig. 4. Vertical section through "hymeneal" fold in a 35 cm. pig, × 25. (1) Circular muscle of Müllerian vagina; (2) circular muscle surrounding Wolffian vagina and separated from the first layer by a connective tissue septum. Mallory triple connective tissue stain.

epithelium. The vaginal wall a short distance above the level of the fold is lined with a single layer of columnar cells. Probably this part of the vagina does not become stratified until the time of sexual maturity. Wilson (10) describes it to be three or four cells thick in the adult pig at the resting stage of the sexual cycle. The muscular coat of the upper part of the vagina consists mainly of bundles of smooth muscle circularly arranged. External to this layer are a few longitudinal bundles. At the level of the hymen a new layer of circularly disposed smooth muscle is found which replaces the other. It lies outside the circular stratum of the upper part of the vagina and is separated from it by a definite connective tissue septum. Both layers are, however, internal to the stratum vasculare. At the region of the opening of the urethra into the

urogenital sinus, striated muscle fibres from the pelvic floor are found to blend with this second layer of smooth muscle.

DISCUSSION

It has been shown in the foregoing description that, developmentally considered, there are three regions in the vagina of the pig: (1) an upper portion which is formed from the lower part of the tubular utero-vaginal canal; (2) below this, there is a region, quite short and narrow, derived from the solid tips of the Müllerian ducts; and (3) next the sinus is a median canal into which open the Wolffian ducts (ducts of Gärtner in the adult). I propose now to consider each of these parts and I shall designate them, for convenience, the upper, the middle, and the lower vaginal segments.

Upper segment. This part is formed from the fused Müllerian ducts in the lower portion of the genital cord. It has for long the form of a simple epithelial tube lined by a single layer of columnar cells. During development numerous vertical ridges are formed on its inner surface. The transformation of the columnar epithelial lining into a stratified one commences very late in foetal life and is first to be observed at the lower end. From this part it spreads slowly and irregularly upwards, and probably does not reach the cervix until the time of sexual maturity. It is noteworthy that this segment of the vagina never becomes solid during development; and in this, as also in the slow transformation undergone by its epithelium, it is in strong contrast with the upper part of the vagina in the human female. The retention of the primitive tubular condition in the upper region of the vagina seems to be the rule in lower mammals (it is found at least in several rodents, in some bats, and in the mole); but to what extent this segment of the vagina is represented in higher forms, if at all, can be determined only by the study of vaginal development in the primates.

Middle segment. The lower ends of the Müllerian ducts are separate from one another in the early stages of development, and union between them does not occur until the foetus has attained a considerable size (17·5 cm.). When first observed the separated parts are solid at their tips, being formed there of polyhedral epithelial cells. According to Nägel (11) this solid condition is to be expected, since these structures represent the growing parts of the Müllerian ducts. At first these cell masses are in contact with the dorsal sinus recesses or bays which, as I have already mentioned, I believe to be the expanded funnel openings of the Wolffian ducts; later, the lower end of each duct is fused with a small diverticulum from the median (Wolffian) canal of the lower segment (12·4 cm. stage). This diverticulum is later drawn out on each side into an epithelial cord, the cells of which are different in appearance from those of the middle segment proper. (These diverticula are further referred to below.) The lower separated rudiments of the middle segment remain short, become flattened antero-posteriorly and may be termed Müllerian vaginal cords (Plate I, fig. 6). Union of these cords in the middle line occurs about the 17·5 cm.

stage, and subsequent canalisation gives rise to the constricted part of the vagina which is the "hymen." My preparations do not show canalisation to have occurred at, or before, the 18·2 cm. stage. This does not agree with the observations of MacCallum (12), who studied the Wolffian body and ducts by the injection of colouring masses into the allantois. He noted that the Müllerian ducts could be injected by this means in female foetuses of the pig measuring 120 mm. C.R. length or more. The pressure employed in this procedure might force a passage between the two parts of the vagina before the histological appearances of canalisation are to be appreciated. It seems certain to me, however, that no *functional* communication exists between the two parts up to the 18·2 cm. stage.

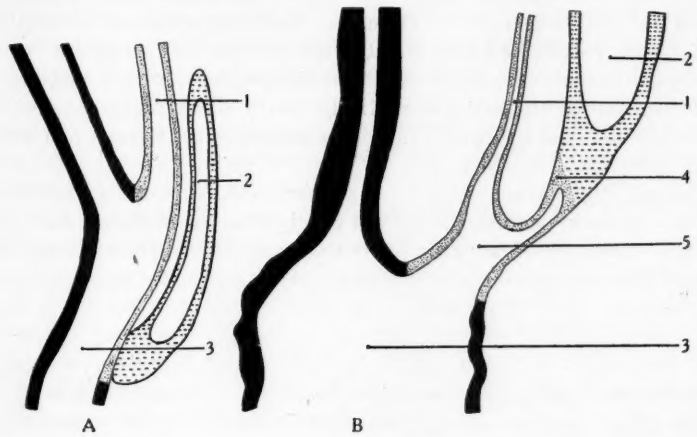
The situation of the "hymen," marking out as it does the lower limit of the Müllerian element in the vagina and delimiting this from the Wolffian contribution below, is precisely what I have previously described for the "hymen" in the rabbit. Here, in the pig, the "hymen" is again seen to be placed at the boundary zone between the actively growing Müllerian segment above and the Wolffian duct segment below. The hymen in the human female (in which form it has been most closely studied) would seem to be formed between the urogenital sinus below and whatever structures form the vagina above. What these vaginal component parts are seems to me to be still undetermined in spite of the large amount of work upon the subject. It is therefore not yet possible to say if the hymeneal structures in these lower forms (pig and rabbit) have the same developmental relationships as in the human subject. These would be truly homologous only if the human vagina were a simple structure wholly derived from the Müllerian ducts.

Lower segment. This portion of the vagina develops rather later than the other parts. The rudiment of it can be recognised at the 8·2 cm. stage, and it is well developed in a foetus of 12·4 cm. C.R. length, where it forms a median canal interposed between the Müllerian ducts and the urogenital sinus. The formation of this canal appears to me to have been the result of the union from above downwards of the two ridges found on the lateral wall of the sinus in the 8·2 cm. stage. The lower ununited ends of these folds are to be seen in Plate I, fig. 5.

Text-fig. 5 shows that there has been a "descent" of the Wolffian ducts relative to the Müllerian ducts during the formation of the lower segment, but the original contact area between the Müllerian ducts and the dorsal (Wolffian) wall of the sinus remains the same. The Müllerian ducts consequently appear to fuse with two projections from the dorsal wall of the median canal, and further growth causes these projections to be drawn out into cords each continuous above with a Müllerian epithelial cord. When these cords fuse the fusion process is continued and involves the Wolffian cords of the lower segment as well.

Two structures may enter into the formation of the lower vaginal segment, namely, the Wolffian ducts and the urogenital sinus. My preparations would

indicate that the Wolffian ducts form this part of the genital canal. Harris (13) has drawn attention to the fact that the dorsal wall of the urogenital sinus as far down as Müller's tubercle is mesodermic in origin, being derived from the Wolffian ducts in the series of changes which result in the formation of the base of the bladder. If this is so for the pig (and my specimens indicate it), the Müllerian ducts come in contact at their lower ends not with the urogenital sinus but with the Wolffian contribution to this structure. When the median canal is formed by union of the two sinus folds at least the dorsal wall of this canal is Wolffian, and the Wolffian element is certainly increased by the changing relationship of the Wolffian ducts to the Müllerian ducts. The cords of the lower



Text-fig. 5. Paramedian sections through the vaginal anlagen and related structures in A an 8·2 cm. foetus, and B a 12·4 cm. foetus. The drawings have been made from graphic reconstructions at the same magnification and represent comparable parts in the two stages. For convenience the Wolffian duct is represented as lying entirely in the plane of section in B; actually its upper part is further lateral. (1) Wolffian duct; (2) fused Müllerian ducts; (3) uro genital sinus; (4) Wolffian epithelium with which tips of Müllerian ducts lie in contact; (5) median canal formed by Wolffian ducts.

segment result from the drawing out of the Wolffian epithelium at the original contact point, and at the same time more and more of the lower end of the Wolffian ducts must be unrolled into the roof and anterior wall of the median canal. The histological difference between the epithelium of the median canal and the epithelium of the sinus in foetal life would also suggest that they are of different derivation. The apparently anomalous relationship of the Wolffian ducts to the lower ends of the Müllerian ducts requires further investigation, and I hope to make this the subject of a subsequent communication. At present it may be noted that all the growth processes involving the lower ends of the Wolffian ducts in the pig seem to be delayed. Examination and reconstruction of earlier stages in my possession show that the base of the bladder

is late in formation, the ureters in a 35 mm. embryo still opening into the Wolffian ducts.

The conditions I have found at the 12·4 cm. stage confirm Wood-Jones' observations, namely, that at this time a canal is interposed between the lower ends of the Müllerian ducts and the urogenital sinus, and my specimens support his hypothesis that this canal is probably derived from the Wolffian ducts.

It may be thought that the formation of the lower vaginal segment by a frontal septum in the sinus is the process observed by Henneberg. It does not seem from Henneberg's description, however, that he actually observed anything more than a descent of the point of union between the urethra and the vagina from the level of the upper border of the symphysis pubis to below the level of the lower border of that structure. Such a descent undoubtedly takes place, but the conditions I have found do not warrant the assumption that it is entirely due to septum formation in the urogenital sinus. On the contrary, the septum formed in the sinus is relatively small, and the real process that Henneberg observed is, I would suggest, a descent of the bladder and urethra towards the pelvis.

This investigation has not lent any support to the view of Felix and Bühler that the vagina in ungulates is derived wholly from the Müllerian ducts. The "hymen" limits the Müllerian contribution, and this structure is found some distance from the opening of the vagina into the urogenital sinus.

CONCLUSIONS

1. The development of the vagina has been investigated in the pig (*Sus scrofa*). Three distinct regions have been recognised which differ in their development. For convenience these have been called the upper, the middle, and the lower vaginal segments.

2. By the fusion of the Müllerian ducts in the genital cord there is formed a simple epithelial tube which is the utero-vaginal canal. The lower part of this tube is the anlage of the upper segment of the vagina. The wall of this tube becomes folded during development so that a number of vertical ridges are formed in this part. The epithelial lining commences to become stratified at the lower part of this segment late in foetal life, and this change spreads very gradually upwards. Even in a young sow, 35 cm. in length, the major portion of the upper vaginal segment is lined with a single layer of columnar cells.

3. The lower ends of the Müllerian ducts do not fuse with each other until the foetus is about 17·5 cm. in length. Each duct tip is in contact with the dorsal wall of the sinus, and each is solid through the proliferation of the constituent epithelium. In this way two short Müllerian vaginal cords are formed. These fuse with each other in the middle line and the resulting structure becomes canalised shortly before or at birth. This part of the vagina remains narrow and forms a hymen in the vaginal canal. It has been termed the middle vaginal segment.

4. The lower end of each Wolffian duct has a funnel-shaped opening into the urogenital sinus. The posterior wall of this funnel (with that of the opposite side) forms the dorsal wall of the urogenital sinus down to, and including, the area where the Müllerian ducts are in contact with the sinus. The funnel openings of the two Wolffian ducts are narrowed by the union of two side-wall sinus folds. The result is the formation of a median Wolffian canal interposed between the Müllerian ducts and the sinus. Disproportionate growth between the Müllerian ducts on the one hand and the Wolffian ducts and urogenital sinus on the other hand causes the tips of the Müllerian ducts to draw out two Wolffian cords from the dorsal aspect of the median canal. These cords fuse with one another in the middle line just later than the Müllerian vaginal cords, and the resulting structure is canalised before or at birth. The median canal and the two cords derived from it form the lower vaginal segment into which open the persisting Wolffian ducts.

5. It is pointed out that the upper vaginal segment of the pig and other lower mammals may not correspond at all with the upper part of the vagina in higher forms. The late persistence of a columnar epithelial lining to this part is also indicated.

6. The hymen in this form is situated in the vagina. It marks off the Müllerian element in the vagina from the Wolffian element lying below, and thus has a similar situation to the hymen in the rabbit. Whether these hymeneal structures in lower mammals have the same developmental relationships as the hymen in the human female is uncertain in the light of recent work on the development of the human vagina. The hymen in the human would seem to differ in that it is developed between the sinus below and whatever structure or structures form the vagina above.

It is with pleasure that I acknowledge the kindness of Prof. Walmsley in providing facilities for, and supervising, this investigation. I have also to thank Miss M. E. Rea for text-figs. 1, 2 and 5.

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EXPLANATION OF PLATE I

Fig. 1. Transverse section of the lower part of the genital cord in an 8·2 cm. female pig foetus, × 86. (1) Dorso-lateral sinus bay; (2) fused Müllerian ducts.

Fig. 2. Transverse section of the lower part of the genital cord in a female foetus of 12·4 cm. C.R. length, × 86. (1) Wolffian duct; (2) Wolffian epithelium on anterior aspect of the right Müllerian vaginal cord; (3) Müllerian vaginal cord.

Fig. 3. A section 75 microns caudal to the preceding one at the same magnification. Lettering as in fig. 2.

Fig. 4. A section 75 microns further caudal in the same foetus showing the union of the Wolffian ducts to form the upper part of the median canal. A few Müllerian cells are to be seen on the dorsal aspect of the fused ducts.

Fig. 5. Transverse section of the genital cord in the same foetus showing the opening of the fused Wolffian ducts into the urogenital sinus. (1) Urogenital sinus; (2) fused Wolffian ducts.

Fig. 6. Coronal section of the lower part of the genital cord in a female foetal pig of 17·5 cm. C.R. length, × 25. (1) Müllerian vagina; (2) Müllerian vaginal cord; (3) median canal formed by fusion of Wolffian ducts; (4) Wolffian duct. Owing to spiral twisting of the vagina around the urethra this section does not appear as if truly coronal.

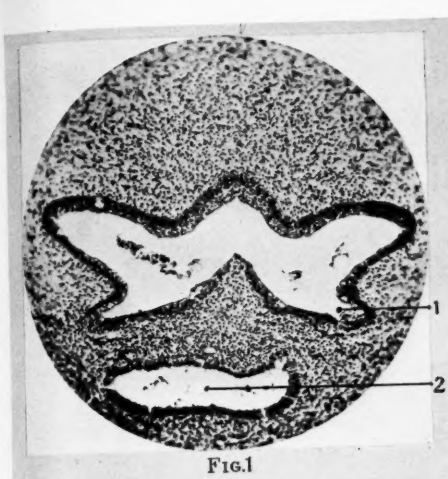

FIG.1

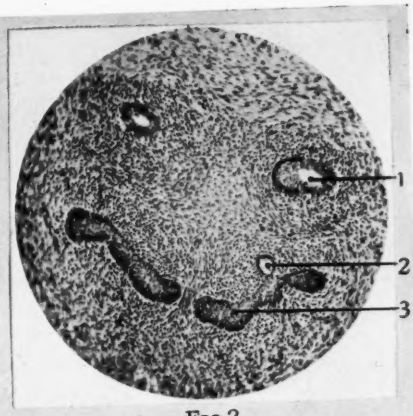

FIG.2

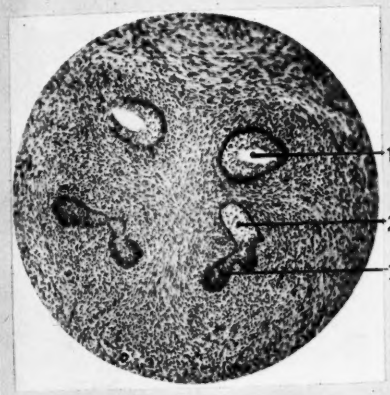

FIG.3

FIG.4

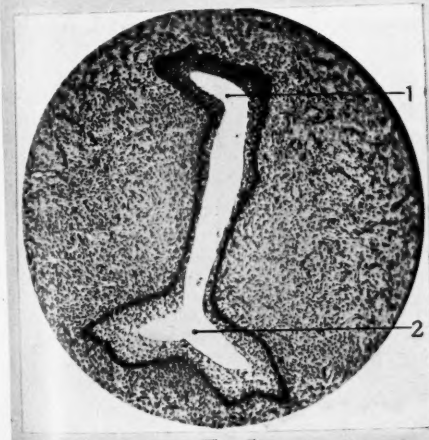

FIG.5

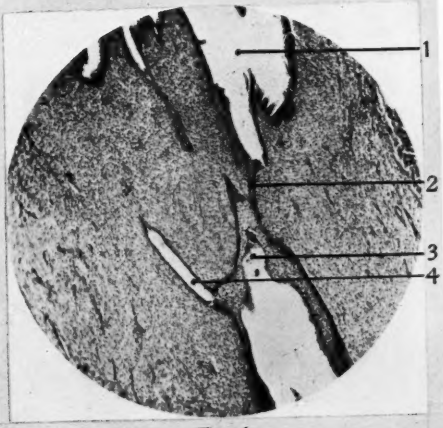

FIG.6

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A RHYTHMICAL PERIODICITY IN THE MITOTIC DIVISION OF ANIMAL CELLS

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A periodic 24-hourly rhythm has often been observed in the karyokinesis of plant cells. Different forms of plant life show a maximum number of mitoses occurring chiefly at night, and a minimum in the daytime. The relative difference between maximum and minimum varies from plant to plant, as does also the hour at which the extremities of the curve are attained.

Karsten (9) has shown that in *Spirogyra*, a maximum number of mitoses occurs about midnight. Kellicott (10), working with *Allium*, found a double rhythm, a primary maximum at 11 p.m. and a primary minimum at 7 a.m., with a secondary maximum and minimum at 1 and 3 p.m. respectively. Stålfelt (13) observed in the roots of *Pisum sedativum* under constant outward conditions a daily rhythm with a maximum about 9–11 in the morning and a minimum about 9–11 at night.

This rhythm is, however, not invariably found. Karsten observed a periodical karyokinesis in the young buds of *Zea Mais*, reaching a maximum during the night, but in the root tips of *Vicia Faba* no such rhythm was to be found. He concluded that *root* growth is non-periodic ("entbehrt der Periodizität"). Berinsohn (1), however, working with *Allium Cepa*, found that the root tips showed more cell division in the dark than in the light. On the other hand, Friesner (6), examining a variety of seedlings and roots from germinating bulbs, found a number of oscillations, as a rule three, in the 24-hour period, and came to the conclusion that the occurrence of maxima and minima in the mitotic curve was dependent not on the time of day by the clock but on the time of initiation of metabolic activity.

A great deal of work has been done on the details of karyokinesis in the animal world, and on the various possible causes which induce or inhibit it. But I have been able to find very little reference to the possibility of a periodic rhythm such as has been observed in plant cells. Mrs Droogleever Fortuyn-van Leyden (3) has, however, investigated this point. She used for her first observations six newly born kittens from two different litters. These were killed at intervals of 4 hours on the second day of life. She does not mention the conditions of temperature or of light, though the light was, by inference, the ordinary light of night and day. In the mesentery, mitoses began to appear at 2.30 p.m., increasing in number till 2.30 a.m. In the crypts of Lieberkühn, the maximum was at 6.30–10.30 p.m., the minimum at 10.30 a.m. In a second series of observations, again on kittens, she records her findings in the thymus, lymph gland and spleen. A maximum number of mitoses was found from 10.30 p.m. to 2.30 a.m., and a minimum at 10.30 a.m. The bone marrow of

these animals showed a maximum at the same time, i.e. 10.30 p.m.–2.30 a.m., but the minimum occurred at 2.30 p.m. Six mice were also examined. Their parentage was not known, and lighting and temperature conditions are again not mentioned. The crypts of Lieberkühn in the mouse had a maximum number of mitoses at 11 a.m. and a minimum at 3 a.m.

Mrs Fortuyn-van Leyden, therefore, found a periodic 24-hourly rhythm in the karyokinesis of cats and mice, though the hour of the maxima and minima varied for the two animals, and to a lesser extent for different tissues in the same animal. The number of observations was small, and in criticism of the results one might say that the animals were of different parentage, thus increasing the chance of individual variations, and no effort apparently was made to stabilise temperature conditions.

This paper records, firstly, observations on eight litters of mice for the purpose of confirming Fortuyn-van Leyden's results. The animals in each series belong to one litter only. The lighting conditions for the doe before birth and for the litter were of the natural diurnal sequence. They were all killed in the same way—by chloroform. Immediately after death, a square piece of skin was cut from the lower part of the right side of the abdomen, and fixed at once in Carnoy's fluid. I would like to emphasise that removal of the tissue and fixation were both done with the minimum of delay, in view of the suggestion that cells undergoing mitosis might complete their division if fixation were delayed. Four hours after fixation in Carnoy, the tissues were changed into 96 per cent. alcohol. Though the method used was the same in each case—this fixative having been found by preliminary trial and error to be the most suitable—the results varied considerably, and in one, fixation was so poor that the colon, which had been removed at the same time, was used instead.

The percentage number is based in every case on a count of 5000 cells, made on five different groups of 1000. The epithelial cells of the epidermis and hair follicles were counted. Cells which are beginning or completing karyokinesis present difficulties to the observer. All the counts were made by myself, so that the same standard, as far as possible, was applied in each case. In cases 1, 2 and 3, no endeavour was made to stabilise the temperature of the surroundings.

Case 1. A litter of white mice. The first of the litter was killed about 8 hours after birth. The skin was examined. The percentage of mitoses was as follows[1]:

12	o'clock	...	...	0·4
16	„	...	...	0·6
20	„	...	...	2·1
0	„	...	...	2·0
4	„	...	...	0·2
8	„	...	...	0·6

[1] The continental mode of counting the hours of the day as 1 to 24, instead of two series of 1 to 12, has been used to avoid confusion.

Case 2. A litter of white mice. The first was killed about 24 hours after birth. The skin was examined. The percentage of mitoses was as follows:

12	o'clock	...	...	0·8
16	,,	...	...	1·3
20	,,	...	...	2·3
0	,,	...	...	2·0
4	,,	...	...	1·5
8	,,	...	...	1·1

Case 3. A litter of white mice. The first was killed about 36 hours after birth. The skin was examined. The percentage of mitoses was as follows:

12	o'clock	...	...	0·8
16	,,	...	...	0·7
20	,,	...	...	1·9
0	,,	...	...	1·3
4	,,	...	...	1·2
8	,,	...	...	0·6

As it struck me after these results that the differences in growth rate might be due to the varying temperature of the surroundings, the animals from now on were kept as far as possible at a constant temperature, the variation never being more than 8° F.

Case 4. A litter of white mice. The first was killed about 48 hours after birth. The skin was examined. The temperature of the room was 70° F. at night and 75° F. by day. The percentage of mitoses was as follows:

12	o'clock	...	...	0·5
16	,,	...	...	0·4
20	,,	...	...	0·8
0	,,	...	...	1·0
4	,,	...	...	0·9
8	,,	...	...	0·5

Case 5. A litter of white mice. The first was killed about 24 hours after birth. The skin was examined. Temperature conditions as in case 4. The percentage of mitoses was as follows:

12	o'clock	...	...	0·4
16	,,	...	...	0·6
20	,,	...	...	1·3
0	,,	...	...	1·2
4	,,	...	...	1·1
8	,,	...	...	0·6

Case 6. A litter of white mice. The first was killed 6 days after birth. The skin was examined. Temperature conditions as in case 4. The percentage of mitoses was as follows:

12	o'clock	...	...	0·6
16	,,	...	...	0·6
20	,,	...	...	1·1
0	,,	...	...	1·2
4	,,	...	...	1·0
8	,,	...	...	0·6

Case 7. A litter of white mice. The first was killed 7 days after birth. The skin was examined. Temperature: 58° F. by night, 63° F. by day. The percentage of mitoses was as follows:

12	o'clock	...	...	0·4
16	,,	...	...	0·6
20	,,	...	...	1·1
0	,,	...	...	1·1
4	,,	...	...	0·9
8	,,	...	...	1·0

Dr L. D. H. Buxton now suggested to me the possibility that the curve was not, as I had taken for granted, a 24-hourly one, but conceivably stretched over a longer period. I waited for a litter of eight, and counted eight periods at 4-hourly intervals.

Case 8. A litter of white mice. The first was killed 3 days after birth. The temperature variation was 70–72° F. The skin was used. The percentage of mitoses was as follows:

12	o'clock	...	...	1·1
16	,,	...	...	1·2
20	,,	...	...	1·4
0	,,	...	...	1·4
4	,,	...	...	0·9
8	,,	...	...	0·8
12	,,	...	...	1·1
16	,,	...	...	1·3

The 24-hourly rhythm continued to hold good.

If the average of the figures is taken for the eight cases the following is the result:

12	o'clock	...	...	0·6
16	,,	...	...	0·75
20	,,	...	...	1·5
0	,,	...	...	1·4
4	,,	...	...	0·95
8	,,	...	...	0·7

Represented graphically, the curves for the eight cases run as in figs. 1 and 2.

The result of these observations on mice is to confirm those of Mrs Droogleever Fortuyn-van Leyden. A daily periodic rhythm is observed, with a maximum between 8 p.m. and midnight, and a minimum at midday.

In 1876 Strassburger (14) found that if *Spirogyra* was left in an unheated room at night, and the temperature sank below 5° C., cell division was delayed until next morning, when on the room being warmed, it took place in full daylight. No inhibition of cell division seems to have occurred in the present

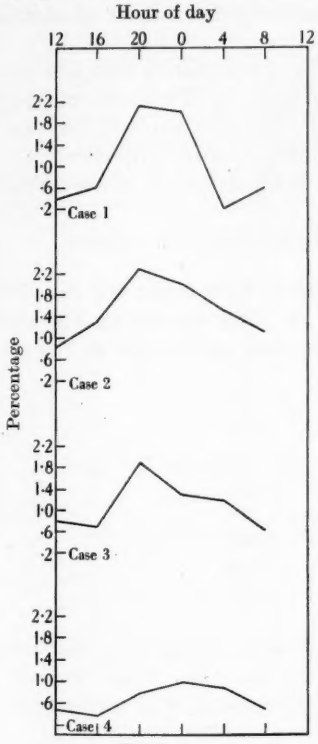

Fig. 1.

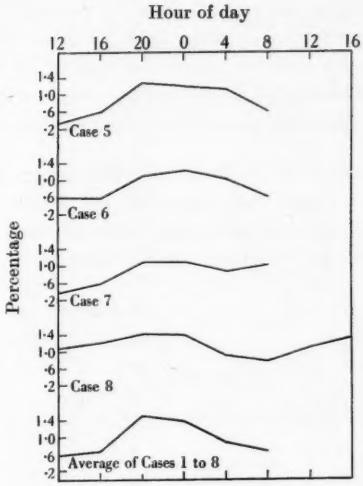

Fig. 2.

case, from the slight lowering of the nocturnal temperature, to which the mice were subjected.

As in each of these eight cases, the mice belonged to the same litter, received the same food, i.e. their mother's milk, and suffered only slight variations of temperature, it seemed possible that the periodic rhythm was caused by the differences in illumination.

Fortuyn-van Leyden (3) observed that if growing onions were kept in the dark in a box, the lowest and highest points of the periodic curve occurred at 7 p.m. and 11 a.m. respectively, whereas under ordinary conditions these points were at 11 p.m. and 7 a.m.

Karsten (9) in his work already mentioned on the root tips and growing buds of various plants found that:

(1) Continuous exposure to electric light eliminated the period and inhibited growth.

(2) Irradiation with an electric lamp at night, with darkness by day, gave two maxima instead of one, with a time difference of 12 hours. He suggested the presence of two warring factors, firstly, an inheritance factor from parents accustomed to the natural diurnal variation, and secondly, a direct adaptation to the changed conditions.

To test the effect of varying light conditions, several litters were now kept in a dark room and exposed at intervals to the light of a 75 watt electric lamp hanging over the cage at a distance of 38 in. When not exposed, the cages were protected from light by loose wooden covers. Four-hourly counts were made, as before, over a period of 24 hours, but whenever a larger litter than six presented itself, further counts were made.

The following three cases were exposed to continuous illumination.

Case 9. A litter of white mice. Exposure to light began the day after birth, and was continued for 7 days, when the litter was killed. The temperature variation was minimal, 70–71° F. The skin was examined. The percentage of mitoses was as follows:

12	o'clock	...	...	0·9
16	,,	...	...	1·3
20	,,	...	...	0·7
0	,,	...	...	0·8
4	,,	...	...	0·9
8	,,	...	...	0·6
12	,,	...	...	0·9

Case 10. A litter of white mice. Exposure to light began the day after birth, and was continued for 7 days, when the litter was killed. The temperature variation was 62–70° F. The skin was examined. The percentage of mitoses was as follows:

12	o'clock	...	...	0·7
16	,,	...	...	0·9
20	,,	...	...	1·5
0	,,	...	...	1·0
4	,,	...	...	1·1
8	,,	...	...	1·1
12	,,	...	...	1·2
16	,,	...	...	0·9

Case 11. A litter of white mice. Exposure to light began the day after birth, and was continued for 8 days, when the litter was killed. The tem-

perature variation was 62–70° F. The skin was examined. The percentage of mitoses was as follows:

12	o'clock	...	...	0·8
16	,,	...	...	0·7
20	,,	...	...	0·8
0	,,	...	...	0·8
4	,,	...	...	0·8
8	,,	...	...	0·9
12	,,	...	...	0·9

These results agree with those of Karsten, already referred to, in that the periodicity is eliminated by continuous exposure to light; but the inhibition of growth which he noted in plants is only observed in case 11. There is a sudden irregular rise at 16 o'clock in case 9, and 20 o'clock in case 10, but no steady wave. If an average is taken of the figures in these three cases, the following results are found:

12	o'clock	...	...	0·8
16	,,	...	...	1·0
20	,,	...	...	1·0
0	,,	...	...	0·9
4	,,	...	...	0·9
8	,,	...	...	0·9
12	,,	...	...	1·0
16	,,	...	...	1·0

In fact, the periodicity has been completely eliminated.

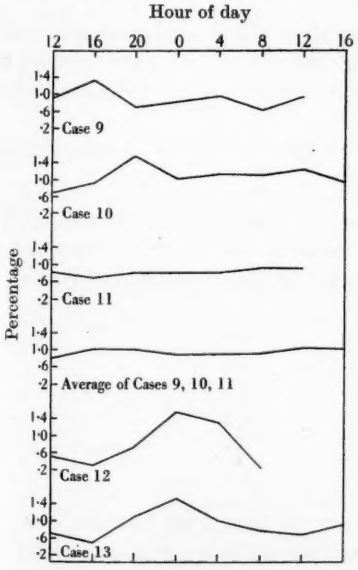

Fig. 3.

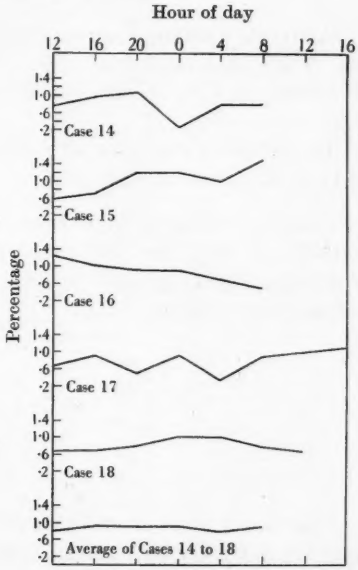

Fig. 4.

The next two cases were kept in continuous darkness.

Case 12. A litter of black and white rats. Weaned 23 days after birth, and then kept in darkness for 14 days. They were fed on mixed corn, brown bread, lettuce and liver. The temperature variation was minimal, 70–71° F. The skin was examined. The percentage of mitoses was as follows:

12	o'clock	...	...	0·5
16	„	...	...	0·3
20	„	...	...	0·7
0	„	...	...	1·5
4	„	...	...	1·3
8	„	...	...	0·2

Case 13. A litter of white mice. Kept in continuous darkness for 7 days after birth, and then killed. The temperature variation was 62–70° F. The skin was examined. The percentage of mitoses was as follows:

12	o'clock	...	...	0·7
16	„	...	...	0·5
20	„	...	...	1·1
0	„	...	...	1·5
4	„	...	...	1·0
8	„	...	...	0·8
12	„	...	...	0·7
16	„	...	...	0·9

Continuous darkness appears hardly to affect the normal diurnal periodicity. There is, however, a "lag." The minimum is at 16 o'clock instead of 12 o'clock, and the maximum at midnight instead of 20 o'clock to midnight.

The following five cases were exposed to light from 11 or 12 o'clock noon to 11 or 12 o'clock at night.

Case 14. A litter of white mice. Exposed to light from 3 days after birth, and killed 10 days later. The temperature variation was 70–71° F. The fixation of the skin was so bad that the colon was used for counting. The percentage of mitoses was as follows:

12	o'clock	...	...	0·8
16	„	...	...	1·0
20	„	...	...	1·1
0	„	...	...	0·3
4	„	...	...	0·8
8	„	...	...	0·8

Case 15. A litter of white mice. Exposed to light from 11 to 23 o'clock, from the day after birth, and killed 8 days later. The temperature variation

was 70–71° F. The skin was examined. The percentage of mitoses was as follows:

12 o'clock	...	...	0·6
16 „	...	...	0·7
20 „	...	...	1·2
0 „	...	...	1·2
4 „	...	...	1·0
8 „	...	...	1·5

Case 16. A litter of white mice. Exposed to light from 12 to 0 o'clock from the day of birth for 10 days, and then killed. The temperature variation was 65–70° F. The skin was examined, and the percentage of mitoses was as follows:

12 o'clock	...	...	1·2
16 „	...	...	1·0
20 „	...	...	0·9
0 „	...	...	0·9
4 „	...	...	0·7
8 „	...	...	0·5

Case 17. A litter of white mice. Exposed to light from 12 to 0 o'clock for 7 days after birth, and then killed. The temperature variation was 62–70° F. The skin was used, and the percentage of mitoses was as follows:

12 o'clock	...	...	0·7
16 „	...	...	0·9
20 „	...	...	0·5
0 „	...	...	0·9
4 „	...	...	0·3
8 „	...	...	0·9
12 „	...	...	1·0
16 „	...	...	1·1

Case 18. A litter of white mice under exactly the same conditions as the preceding case. The skin was used, and the percentage of mitoses was as follows:

12 o'clock	...	...	0·7
16 „	...	...	0·7
20 „	...	...	0·8
0 „	...	...	1·0
4 „	...	...	1·0
8 „	...	...	0·8
12 „	...	...	0·7

If we take the average results of these five cases, the figures are as follows:

12 o'clock	...	...	0·8
16 ,,	...	...	0·9
20 ,,	...	...	0·9
0 ,,	...	...	0·9
4 ,,	...	...	0·8
8 ,,	...	...	0·9

The effect of retarding the normal period of illumination to a later hour of the day seems to have been to destroy the periodicity completely.

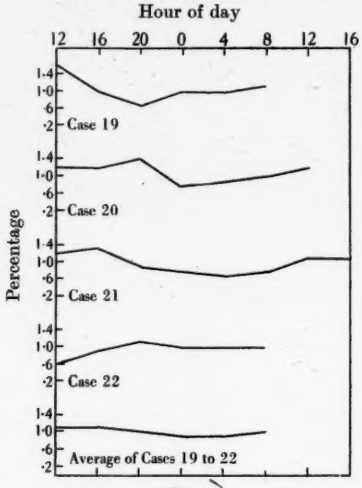

Fig. 5.

The following four cases were exposed to light from 11 or 12 at night to 11 or 12 noon.

Case 19. A litter of white mice. Exposed to light from 23 to 11 o'clock from the day of birth for 5 days, and then killed. Temperature variation 70–71° F. The skin was examined, and the percentage of mitoses was as follows:

12 o'clock	...	...	1·6
16 ,,	...	...	1·0
20 ,,	...	...	0·7
0 ,,	...	...	1·0
4 ,,	...	...	1·0
8 ,,	...	...	1·1

Case 20. A litter of white mice. Exposed to light from 0 to 12 o'clock from birth for 8 days. Temperature variation 62–70° F. The skin was examined, and the percentage of mitoses was as follows:

12	o'clock	...	...	1·2
16	,,	...	...	1·2
20	,,	...	...	1·4
0	,,	...	...	0·8
4	,,	...	...	0·9
8	,,	...	...	1·0
12	,,	...	...	1·2

Case 21. A litter of white mice. Exposed to light from 0 to 12 o'clock from the day of birth for 8 days. Temperature variation 62–70° F. The skin was examined, and the percentage of mitoses was as follows:

12	o'clock	...	...	1·2
16	,,	...	...	1·3
20	,,	...	...	0·9
0	,,	...	...	0·8
4	,,	...	...	0·7
8	,,	...	...	0·8
12	,,	...	...	1·1
16	,,	...	...	1·1

Case 22. A litter of white mice. Conditions as in preceding case. Percentage of mitoses as follows:

12	o'clock	...	...	0·6
16	,,	...	...	0·9
20	,,	...	...	1·1
0	,,	...	...	1·0
4	,,	...	...	1·0
8	,,	...	...	1·0

An average taken from the figures in the last four cases produces the following results:

12	o'clock	...	...	1·1
16	,,	...	...	1·1
20	,,	...	...	1·0
0	,,	...	...	0·9
4	,,	...	...	0·9
8	,,	...	...	1·0

Thus, illumination from midnight to midday causes considerable irregularity and eliminates the periodicity.

An apology appears to be due for the number of apparently purposeless variations in the conditions of temperature, the periods of illumination, and duration of life. There was much difficulty in obtaining material. Litters of mice are often less than six, and thus useless for the present purpose. When they were of six or more, the mother frequently reduced the number of her

brood by eating one or two. The litters had therefore to be taken wherever they were available, and thus the work was done in three different laboratories, in only one of which temperature conditions were stable. Again, when the mice had to be changed every night from dark to light or *vice versa*, one was dependent on the services of the night porter, who did his rounds in one case at 11 o'clock, in another at midnight. And finally, with regard to duration of life the mice had to be killed when one could be free of any other engagements for 24 hours or more.

SUMMARY

1. Under normal conditions of light, there appears to be a 24-hourly rhythm in the mitotic division of animal cells, with a maximum from 8 o'clock in the evening to midnight, and a minimum about noon.

2. This periodicity is destroyed by continuous exposure to light; but not by continuous darkness.

3. Exposure to artificial light for 12 out of the 24 hours causes irregularity in the curve of mitotic division, with a complete suppression of the rhythm (independent of the period of illumination).

4. The numbers of individuals on which the counts were taken are too small for certainty, but the figures are suggestive.

My thanks are due to Prof. Thomson, Department of Human Anatomy, Prof. Dreyer, F.R.S., Sir William Dunn, School of Pathology, Prof. Gunn, Department of Pharmacology, and Prof. Peters, Biochemical Laboratory, for according to me the facilities of their Departments; to Dr L. H. Dudley Buxton for his valuable criticism and suggestions; and to Miss Kempson, Messrs W. Chesterman, Thomas Marsland and Jesse Wheal for assistance in keeping animals, section cutting and staining.

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THE ILEO-CAECAL JUNCTION

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A study of the standard works of Anatomy shows that there is a considerable difference of opinion regarding the form and function of the ileo-caecal junction. Keith (1), Rutherford (2) and Elliott (3) hold that there is a sphincteric mechanism which controls the exit of the ileal contents into the caecum, depending for its efficiency on a sphincteric muscle around the terminal ileum. Symington (4) and Waterson (5) believe that there is a valve-like action of the valvula coli, produced by the obliquity of the entrance of the terminal ileum into the caecum in a manner analogous to the valve-like action of the intramural portion of the ureter, acting in such a manner as to prevent the regurgitation of material from the caecum into the ileum. Struthers (6) thinks that there is a combination of valvular and sphincteric action.

The description of the ileo-caecal junction given by Waterson is as follows: "The valve is made up of two crescentic segments, a superior, labium superius, in a more or less horizontal plane; and an inferior, labium inferius, which is larger, placed in an oblique plane, and sloping upwards and inwards, i.e. towards the cavity of the caecum. Between the two segments is situated the slit-like opening, which runs in an almost antero-posterior direction with a rounded anterior and a pointed posterior extremity. At each end of the orifice the two segments of the valve meet, unite, and are prolonged around the wall of the cavity as two prominent folds...the frenula coli. It is thought that when the caecum is distended, and its circumference thereby increased, the frenula are put on the stretch, and pulling the two segments of the valve, they bring them into apposition, and effect the closure of the orifice."

If a series of specimens of the ileo-caecal region is examined, great variation is seen to exist both in the form of the terminal ileum and in the relation which it bears to the caecum. It is also seen that no single description of this part would be sufficiently comprehensive to cover these variations. As this region marks an important junction between two physiologically different parts of the digestive tube, small intestine and large intestine, an investigation was undertaken to try to discover an explanation for them. The gross anatomical relations of the ileo-caecal junction and the adjacent parts of the small and the large intestines were studied by dissection methods, particularly with reference to the presence or absence of bands of peritoneum binding the terminal ileum to the adjacent parietes; by a method of injecting liquid gelatine into caeca taken from dead bodies; by the microscopic study of sections of the tissue of

this region; and by X-ray photographs of the ileo-caecal junction taken from living persons. The specimens into which gelatine was injected were hardened in formalin, and coronal sections of them were cut in order to study the form and position of the valves, and to learn if the gelatine had passed from the caecum, through the ileo-caecal opening, into the ileum. About 200 specimens were studied in these different ways.

It is not proposed, in this communication, to question the presence of a well-marked ileo-caecal sphincter. Keith has already mentioned the existence of this sphincter, and Beattie (7) has described, in the human embryo, the development of the muscle fibres which constitute it. It is the question of the frenula and their supposed valvular action that is to be considered.

In the case described by Rutherford (2) in which the ileo-caecal valve and caecum were seen through an artificial opening in the abdominal wall, frenula were not observed. But in a later paper Rutherford (8) brings forward evidence to show that true frenula do exist in the human caecum, although they may not be observable in the living body under the conditions described by him. He states that the apparent absence of frenula is due to the fact that living mucous membrane is much thicker than it is after death, because of the fluids contained in it, and that these tend to conceal the structure of the frenula. The fluids, he argues, are drained off after death and, as a result of post-mortem rigidity, the muscular fibres of the frenula become evident. The formalin preservative also acts on the muscular tissue of the frenula after death, and this action causes its contraction rendering the frenula more distinct.

Rutherford examined a number of caeca for the presence of these frenula, and cut sections at right angles to their long axis, and he found that definite bands of muscle fibres were present in all of them. This muscle tissue, he claimed to be, morphologically, the caeco-colic sphincter of lower forms. But he did not bring forward any evidence to support this claim, other than the sections studied of the human frenula coli. He recognised the presence of the frenula as distinct structures, but he did not make any attempt to discuss their possible function as valves between ileum and caecum.

The presence of muscle fibres in the frenula cannot be denied. They may be observed in cut and stained sections. Further, in all mammals a well-marked caeco-colic sphincter is always present, situated at a variable distance above the level of the ileo-caecal sphincter, and in none of them is there any trace of the frenula, microscopically or macroscopically, either during life or after preservation in formalin or other fixative. The ileal opening appears as a raised papilla on the medial wall of the caecum, and a true sphincteric ring closes off the upper end of the caecum from the colon (fig. 1). The study of this region in a series of mammalian types shows (fig. 2) that the distance between the ileo-caecal and caeco-colic sphincters diminishes with the changing form of the colon, from the simple carnivorous and the complex herbivorous types to that of the large intestine which is common to the mixed feeders. The position of the caeco-colic sphincter, in the human subject, is found at the level of the ileo-

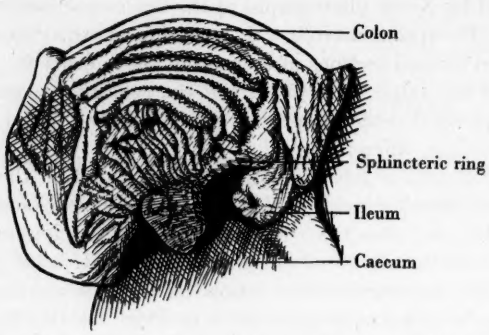

Fig. 1. The caeco-colic junction of the guinea-pig opened from the front to show the well-marked caeco-colic sphincter, with the papilla of the ileal opening into the caecum below the level of the sphincteric ring.

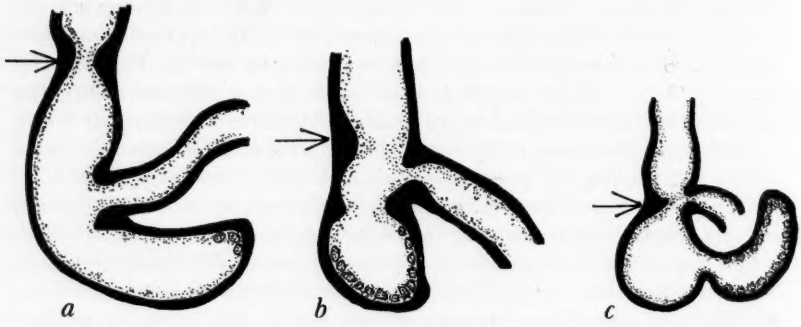

Fig. 2. Three stages in the migration of the caeco-colic sphincter as seen in (*a*) mongoose, (*b*) dog, and (*c*) rat. The position of the caeco-colic sphincter is indicated by an arrow.

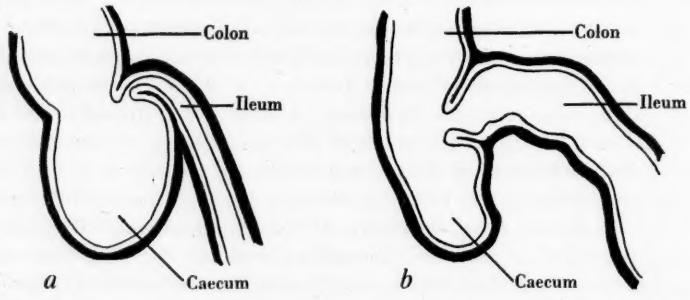

Fig. 3. Diagrams to show the two positions of the terminal ileum. *a*. The oblique ascending position of the empty ileum. *b*. The "horse neck" curve of the turgid ileum.

caecal junction, and there forms the frenula coli in the position described by Rutherford.

If sections are cut from a number of caeca, the lower lip of the ileo-caecal junction will be seen to be longer and more mobile than the upper, and further, in a series of specimens hardened before section, the position of the lower lip will be found to vary directly with the changes in the form and direction of the terminal ileum (fig. 3 *a*, *b*). On making this observation a number of caeca from post-mortem examinations, and from preserved dissecting-room subjects, were injected with hot gelatine, the colon and ileum being first ligatured about 6 in. on either side of the ileo-caecal junction, and the flow of gelatine studied. After the gelatine had hardened in formalin, sections were made through the centre of the ileo-caecal opening, and the gelatine was found to be confined to the caecum in certain of the specimens, but in others it had passed into the ileum and had filled it. Further studies showed that the distribution of the gelatine depended on the direction of the terminal ileum. In some of the specimens the ileum passed from the pelvis obliquely upwards and to the right, flattened against the medial wall of the caecum (fig. 3 *a*), whilst in others it presented a well-formed "horse neck" curve, with the terminal ileum directed more or less at right angles to the medial wall of the caecum (fig. 3 *b*). With these variations in the form and position of the terminal ileum there were also observed corresponding changes in the form of the valvula coli. The specimens in which the ileum curved upwards to meet the caecum with the "horse neck" curve presented valvulae coli as described by Waterson. But in the specimens where the ileum was flattened against the medial wall of the caecum, the lower of the two folds of the valvula was obliterated whether the caecum was in the contracted and empty condition, or dilated and full, and it appeared as a fold of tissue common to the medial wall of the caecum and the terminal ileum. This fold appeared to act as a kind of valve. Pressure within the caecum would cause this fold to be pressed against the mesenteric wall of the terminal ileum and by so doing occlude the ileal opening. It would thus act as a valve and prevent the passage of material from caecum to ileum. This is the suggested explanation for the fact that when liquid gelatine was forced into the caecum under pressure, the gelatine did not pass into the ileum. But in the specimens in which the opening of the ileum was directed more or less at right angles to the medial surface of the caecum, and the ileum formed a "horse neck" curve, the gelatine passed into the ileum. The ileo-caecal opening in these specimens was guarded only by the sphincter, which in the dead specimens had relaxed, leaving open the communication between caecum and ileum. It is of interest to note in this connection that in all the types of mammals studied, in which there was a complete absence of frenulae coli, the terminal ileum passed into the caecum in a plane at approximately right angles to the medial wall of the caecum.

The changing form of the terminal ileum would appear to be a matter of considerable importance in the transmission of food materials from ileum to

caecum. If the caecum is full, contraction of its walls will, with the terminal ileum in the ascending position, cause the lower fold of the frenula to act as a valve and prevent regurgitation into the ileum, and the intra-caecal pressure being transmitted to the caeco-colic sphincter will cause it to open and permit food material to pass into the proximal colon (9). On the other hand, the contents of the terminal ileum, being forced onward, would distend this segment of the gut, which would then tend to "straighten itself out" to form a "horse neck" curve, and finally to reach a position more or less at right angles to the medial wall of the caecum. The pressure by the forced contents of the ileum then would dilate the ileo-caecal sphincter, and the ileal contents would pass into the caecum. This view is in conformity with the X-ray cinematograph pictures taken in the living human subject by Wingate Todd (10). These pictures show that the passage of an opaque meal occurs in "puffs" which occur at the end of the formation of a "horse neck" curve on the terminal ileum.

Confirmatory evidence, that these changes occur in the form of the terminal ileum, is found in those cases of chronic constipation, in whom the terminal ileum and caecum are found at operation to be bound down by peritoneal bands, which prevent the formation of the "horse neck" curve on the ileum. The surgical removal of such bands is said to result in the freedom of the terminal ileum, and to permit the formation of the "horse neck" curve. Through the kindness of Mr T. S. Kirk, of the Royal Victoria Hospital, Belfast, I have been enabled to study a series of case reports of patients from his wards. In all of them where there was a history of chronic constipation and in which, on opening the abdomen, the terminal ileum and caecum were found to be bound down to the pelvic wall, their surgical liberation, by removal of the bands, is claimed to have resulted in the relief of the constipation. In several cases where purgatives had been taken over a number of years in order to relieve constipation, normal daily motions resulted, and the constipation was completely cured.

These morphological facts of the ileo-caecal junction all point to the following conclusions:

1. That the lower fold of the frenula coli acts as a valve to prevent the regurgitation of food material from caecum to ileum, and by thus raising the intra-caecal pressure aids in the opening of the caeco-colic sphincter, which in the human subject is incorporated within the frenula coli.

2. That this valve-like action depends on the position of the terminal portion of the ileum; when the ileum ascends from the pelvis along the medial wall of the caecum, the flap acts as a valve, but when it is raised in the "horse neck" curve, the valve-like action does not occur. It is in this position that the ileo-caecal sphincter opens and permits the passage of food from ileum to caecum.

3. That freedom of movement of the terminal ileum is essential for the free passage of food material from the small to the large intestine.

I should like to acknowledge my indebtedness to Prof. Thomas Walmsley for his kindly criticism and advice during the preparation of this paper.

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COALESCED KIDNEYS IN A RABBIT, AND THE ASSOCIATED ANOMALIES IN THE CIRCULATORY AND NERVOUS SYSTEMS

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The specimen to be discussed, a rabbit exhibiting coalesced kidneys, was one used for dissection in a biology class. Its anomalous structure seemed worth a brief description for several reasons. No previous record of fusion of the kidneys in a rabbit appears in the literature, and no examples have been met with among thousands of specimens that have come under observation in this laboratory during the past thirty years. In Man, moreover, a "vertical" renal fusion, such as obtains in this specimen, is an extremely uncommon condition. Among some 18,000 hospital autopsy records examined by Morris (1), which afforded 19 examples of typical horse-shoe kidney, there was no case of this phenomenon. From collected records of renal anomalies, Dorland (2) quotes 8 cases out of a total of 123, and Gérard (3) quotes 14 out of 527, in none of which did the kidney occupy the middle line, as it does in the present instance.

The anomaly, then, is remarkable as a mere curiosity. But it is also interesting for comparison with the rare human cases that have, in fact, occasionally been brought to light. It has further seemed worth studying for the sake of some apparently embryonic features which it retains in its abnormal renal and vascular systems, and also for modifications in the sympathetic nervous system, which, for the first time in a case of coalesced kidneys, have been traced, and are here described.

GENERAL DESCRIPTION

The rabbit is a small female, probably about 7 weeks old, and normal in external appearance. The dissection of the urinary system was begun while the specimen was still fresh, and while, though parts of the body were no longer intact, these organs were undisturbed. The adrenal glands, ovaries and uteri are normal in structure and position. The fused kidneys form a compact mass, the longitudinal axis of which is parallel to that of the body, and only slightly to the left of the middle line (fig. 1). After preservation the mass measures 31 mm. in total length, 19 mm. in greatest width and about 10 mm. in average thickness, while the corresponding measurements in a single normal kidney would be about 25, 15 and 10 mm. Markedly ectopic, it covers the sixth and

seventh lumbar vertebrae and a part of the first sacral. whereas in the normal animal the right kidney is level with the first lumbar and part of the twelfth thoracic, and the left with the first lumbar and part of the second lumbar. No trace of a kidney exists in either of the usual sites.

The organ closely resembles a single kidney in shape. The anterior (cranial) lobe, however, is superficially marked off from the posterior (caudal) lobe by a slight horizontal groove, nearly complete on both dorsal and ventral surfaces.

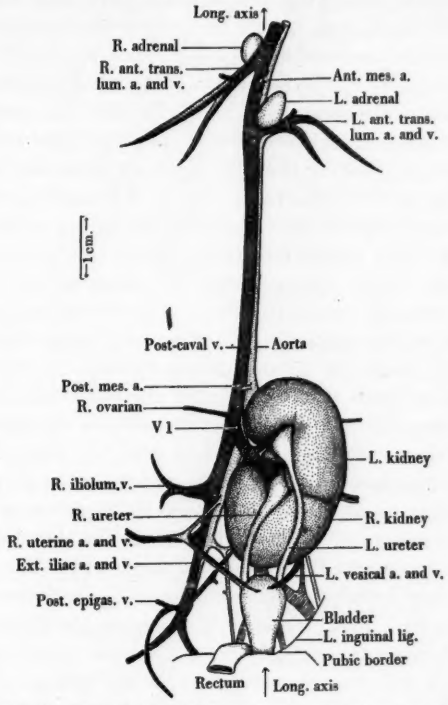

Fig. 1. Ventral dissection showing the fused kidneys *in situ*. Uteri, nerves and minor blood vessels are omitted. The right inguinal ligament is removed. Arteries are shown stippled, veins cross-hatched. *a.* or *A.* artery; *ant. mes.* anterior mesenteric; *ant. trans. lum.* anterior transverse lumbar; *ext. iliac*, external iliac; *iliolum.* iliolumbar; *inguinal lig.* inguinal ligament; *L.* left; *post. epigas.* posterior epigastric; *post. mes.* posterior mesenteric; *R.* right; *v.* or *V.* vein.

A ventro-mesial groove, and a purely ventral depression, both on the right side, represent the two hila more or less merged; but each embraces a distinct pelvis, one related to the cranial lobe and the other, immediately behind it, to the caudal. There are two distinct ureters, and a study of their connections reveals the nature of the renal body. One passes ventrally from the more cranial pelvis to enter the left side of the bladder, and the other from the more caudal pelvis to enter the right side. The openings on the bladder are perfectly

symmetrical. This indicates that we are dealing with a true left kidney in the cranial lobe, and a true right kidney in the caudal.

VASCULAR SYSTEM

The renal body has a completely anomalous vascular system. The renal artery and vein normally arise, from the aorta and post-caval respectively, at about the level of the first lumbar artery. Each vessel should give off an adrenolumbar branch, supplying the adrenal gland and the neighbouring dorsal muscles of the body wall. In the anomalous specimen the adrenolumbar arteries and veins have a normal distribution, but arise directly from the main trunks, in the positions proper to renal vessels (fig. 2). The kidney blood supply is independent of the adrenolumbars, and comprises four special arteries and three veins arising much lower down. The caudal lobe (right kidney) is supplied partly by an artery originating from the right common iliac and passing into the hilum near the more caudal pelvis (fig. 2, *A* 1), and partly by a slender branch from the right internal iliac, entering the kidney on its convex caudal surface (fig. 2, *A* 2). The cranial lobe (left kidney) receives an almost median artery (fig. 2, *A* 3), which springs from the aorta at its bifurcation, and divides into two. One of the subdivisions, *A* 3*a* (shown but not labelled) goes towards the hilum on the right side, its termination being concealed by a vein. The second, *A* 3*b*, passes in on the dorsal surface. A fourth renal artery (fig. 2, *A* 4), springing from what is probably the left vesical artery (damaged in parts), enters dorsally just at the groove between the two lobes.

Some of the lower abdominal and pelvic veins are highly irregular. Thus the right external iliac flows into the post-caval about the length of a vertebra further forward than usual, while that on the left is almost equally displaced, but in the caudal direction. As shown in fig. 2, the iliolumbar veins of the two sides also differ markedly in their arrangement. The caudal lobe of the kidney (true right kidney) is drained by two veins corresponding to arteries *A* 1 and *A* 2. The first (figs. 1 and 2, *V* 1) leaves the hilum near the more caudal pelvis and enters the right external iliac; but unlike the artery it also receives a factor (*V* 1 *b*) from the other lobe of the kidney. It is joined at its base by the ovarian vein. The second renal vein of the right side (fig. 2, *V* 2) passes from the extreme caudal end of the structure into the right external iliac. The cranial lobe (left kidney) has a single vein, *V* 3, which corresponds to artery *A* 3*b*. It passes out from the dorsal surface, unites with the left ovarian vein, and enters the root of the iliolumbar vessel.

NERVOUS SYSTEM

The sympathetic nerves associated with the kidney follow the path of the main (anomalous) renal arteries (fig. 2). A nerve, *N* 1, following artery *A* 1 into the true right kidney, can be traced the whole way to the more caudal of the two superior (anterior) mesenteric ganglia. It has two slight swellings on its course, and has fine anastomoses with a small median ganglion ("X"), and also

with the inferior (posterior) mesenteric. Near the latter it sends out a branch to join a (?) hypogastric nerve that courses along the right common iliac artery. Two nerves, *N* 2 and *N* 3, accompany artery *A* 3*b* into the true left kidney. *N* 2 is a branch of a median trunk which emerges from the inferior mesenteric ganglion. (This trunk could not be traced beyond the bifurcation of the aorta.)

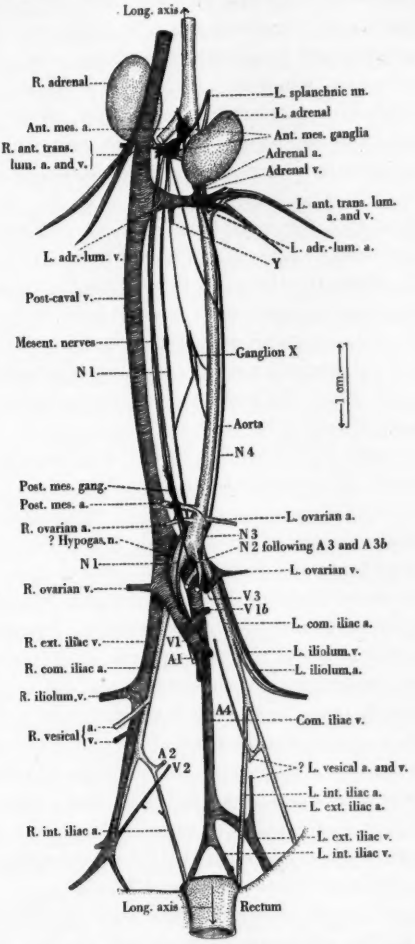

Fig. 2. Dissection after removal of viscera. Post-caval and aorta are pulled away from the middle line to show nerves. With the exception of mesenteric arteries, all blood vessels shown with hollow upturned ends enter the kidneys. Arteries are shown stippled, veins cross-hatched, nerves black. *adr.-lum.* adrenolumbar; *ant. mes. ganglia*, anterior mesenteric ganglia; *com. iliac*, common iliac; ? *hypogas. n.* ? hypogastric nerve; *int. iliac*, internal iliac; *mesent. nerves*, mesenteric nerves; *n.* or *N.* nerve; *post. mes. gang.* posterior mesenteric ganglion; *Y*, vestige of left post-caval (cut near its root); other abbreviations as in fig. 1.

N 3 passes out from a small ganglion lying near the root of the left ovarian artery. A very distinct nerve, *N* 4, running along the aorta, connects this ganglion with a lobe of the more cranial of the two superior mesenteric ganglia.

DISCUSSION

In an attempt to reconstruct the abnormal ontogeny of the specimen, the following topics seem to call for discussion: the evidence for the view that the single renal body was formed by coalescence of the originally paired kidneys; the question of the time at which this fusion occurred, and the question of its cause; the reasons for the remarkably low situation of the fused kidneys, and also for their positions relative to one another; the significance of the orientation of the hila, and the explanation of the various anomalies in the vascular and nervous systems.

It is fairly evident that the renal body is single as a result of fusion of the two kidneys, and not owing to absence of one of them. This is indicated by the slight groove which separates the mass into cranial and caudal lobes, by the existence of a separate pelvis and ureter to each lobe, and by the symmetrical position of the two ureteric openings into the bladder. This last feature rules out the likelihood of the organ's having arisen by duplication of an unpaired left kidney and ureter. Since the more caudal lobe is drained by the ureter on the right of the bladder, and, moreover, derives the whole of its blood supply ultimately from the right iliac artery and vein, it is clear that this lobe represents the right kidney. The other lobe is obviously the left kidney.

The actual time, in the life of the embryo, at which the kidneys fused, can be deduced with a fair measure of probability. It is likely that the appearance of the renal (ureteric) buds was little if at all retarded, for Brown's work on kidney anomalies in mice (4) implies that even a slight delay in the formation of the bud results in complete absence of the kidney. According to Minot and Taylor (5), the buds arise at about the 11-day stage, and have become surrounded by the metanephric blastemata by the end of the 13th day. Evidence suggesting that fusion took place soon after the kidneys were thus laid down, on the 12th and 13th days, lies in their remarkably complete coalescence, and also in the indefinite form of each, and in its incomplete rotation (see below). Further, since the capsular tissue does not pass down into the groove which marks off one kidney from the other, it appears that they united before each had developed its own capsule, i.e. by the 14th day according to Minot (6). They probably, therefore, fused at the end of the 13th day.

If this is the time of their fusion, its cause can be deduced. For according to Hochstetter (7), in the usual course of events on this, the 13th day, the metanephroi lie at first very close together in the fork between the umbilical arteries, and then gradually migrate forward and escape from them. In this anomalous case they must have failed to escape, for in the definitive state they still lie mainly caudal to the common iliac arteries. (The cause of their remaining stationary at that point is discussed below.) Arrested in this confined

space, where they were subject to the lateral pressure of the curved umbilical arteries, they would impinge at or near the middle line as soon as they had grown appreciably in size—apparently by the end of the day. Still plastic in form they would then naturally coalesce.

The etiology of the kidneys' failure to migrate, which has resulted in their exceptionally low definitive position, has two phases. First, there is the above-mentioned stage in which they were held back (between the arteries) before their fusion had actually taken place. The cause of this arrest of migration was probably one of those that are discussed by Lemberger (8). His first hypothesis, namely, that it might be due to failure of the ureters to continue elongating after a certain stage, is unlikely in view of recent researches on mice by Brown (4). This worker finds that early arrest of elongation in the ureters is accompanied by complete cessation of kidney development. A second possibility is that excessive enlargement of each Wolffian body caused its caudal end to adhere to the metanephros, and so prevented the latter from detaching itself. This theory seems applicable here. It is significant, as Lemberger points out, that of all animals investigated, the pig exhibits the largest Wolffian body in the embryo and the highest incidence of dystopic kidney in the adult. Since a rabbit embryo also has exceptionally large Wolffian bodies, it seems not improbable that in the present instance these were responsible during their active period for preventing the upward passage of the kidneys. Hochstetter's figures of the 12-day rabbit embryo (7) show the caudal ends of the mesonephroi terminating close to the kidneys and just at the level of the aortic bifurcation. It is clear that only a slight hypertrophy of these mesonephroi would, in fact, cause the detention of the kidneys between the umbilical arteries, exactly in the locality required if their fusion is to be explained by the hypothesis given above.

Their migration, however, was evidently still impeded even after the Wolffian bodies degenerated. In this second phase, the explanation lies in the fact that as a result of the mode of coalescence the renal body occupied a practically median position. It was thus effectively obstructed, in any movement in a headward direction, by the presence of the mesentery and the inferior mesenteric artery. That this is the probable reason for the permanent dystopia is borne out by a correlation observed in human cases. Thus it appears that nearly all median coalesced kidneys, that have been described, are situated noticeably low (Morris (1)); whereas in conjoined kidneys that lie to one side of the mid-line, the upper pole is generally at its customary level, even when fusion has evidently taken place before the migration stage. Among twenty-two instances of "complete coalescence" collected from the literature by Gérard (3), this correlation seems to have been perfect.

The renal organ of the rabbit under discussion is remarkable for the positions, relative to one another, of the two kidneys composing it. It differs from all the human examples classified by Gérard in that, in spite of lying in a nearly median, very low position, its two components are placed almost

one below the other rather than side by side. Two accounts by Kelly (9) and by Macdonald (10), respectively, afford perhaps the only other records of this combination of features. It would be explained, in the present instance, if the right Wolffian body was more hypertrophied than the left, keeping the right metanephros somewhat caudal to its fellow, in the early phase. The resulting somewhat horse-shoe like, but unsymmetrical, fused mass, being subject to lateral compression, and not being balanced about the mid-line of the body as a perfect horse-shoe is, would tend to rotate slightly in a frontal plane so as to bring its long axis in line with that of the abdominal cavity. Thus the right kidney would come to lie more definitely below the left. The oblique directions taken by the renal vessels indicate that such a shifting may have occurred.

A digression is perhaps permissible here on the subject of the relative positions of the two kidneys in normal adult rabbits, where the right one is very constantly at a higher level than the left. Brown (4) has shown, in mice, that the right-handed caudal twist of the embryo's body has the effect of advancing the migration of the left kidney beyond that of its fellow, and is the cause of the more cranial definitive position of the former. The same bending and the same ultimate relations of the kidneys obtain in the pig. In the rabbit there is an exceptionally marked bend to the left, amounting by the middle of the 11th day to a spiral twist (Minot and Taylor (5)). It seems reasonable to infer that this causes the asymmetrical position of the kidneys in the adult rabbit[1]. In the anomalous specimen, the fact that the right adrenal gland is, as normally, cranial to the left, shows that the embryo twisted to the left as usual, and the right kidney lagged in spite of this factor.

As has been shown by Pohlman (11) and others, the orientation of the hila, i.e. degree of rotation about their axes in abnormal kidneys, is noteworthy. The kidney in mice (4), and, to judge by Hochstetter's figures (7), in the rabbit also, takes place just as it is passing forward clear of the umbilical arteries. In the specimen under discussion, the rotation would therefore just be beginning, in the more advanced left kidney, at the time when coalescence was in progress. The fusion would arrest rotation, and leave just such a ventral right hilum, and ventromesial left hilum, as obtain in the definitive state. A closely analogous arrangement of the two hila existed in the human subject described by M'Murrich (12), and slightly different degrees of rotation are evident in Greenfield's (13) and in Coupland's (14) cases. None of these are strictly "sigmoid" kidneys. Greenfield's may possibly have been a displaced horse-shoe.

A few of the anomalies in the blood vascular system are worth referring to briefly. As Bremer (15) has pointed out, after the aorta develops a tunica media, and the kidney its capsule, no new renal arteries can arise. Hence the present arteries supplying the kidney must have been in existence, at least as part of a plexus, on the 13th day. Their source in the iliacs therefore suggests that in the rabbit there may be, at this period, an umbilical-renal capillary connection like that described by Jeidell (16) in the 14 mm. pig.

[1] In Man, the embryonic twist appears to be so slight as not to affect the kidneys in this way.

A significant feature is the union of the principal renal vein on each side with the corresponding ovarian vein. According to Reagan and Tribe (17) the ovarian veins each develop from a transverse element draining the caudal end of the mesonephros. Their connection therefore with the renal veins, in this specimen, implies the existence in the 13-day rabbit of capillaries, again like those of the pig embryo, draining the renal anlage into the posterior mesonephric veins. It must be a relic of these capillaries which connects the renal with the ovarian vessel. The link is, of course, not comparable with a certain connection between these two veins that is frequently found in normal adult rabbits. There the left genital vein, instead of taking the usual direct transverse path dorsal to the aorta, and joining the post-caval opposite the sixth lumbar, may turn at right angles and run forward through five segments to enter the renal vein of the left side. In these cases the entire longitudinal part of the vein is a linking vessel between the true genital and the renal; but it is a relic, not of a capillary anastomosis, but partly of the left post-cardinal and partly of the left post-caval. This has been shown by Hochstetter (7)[1].

A vestige of the left post-caval does indeed exist in the anomalous specimen, but quite separately from the more caudally situated genital vein. It is a minute vessel, running forward close to the abdominal aorta, to enter the left adrenolumbar vein near the junction of the latter with the definitive post-caval (fig. 2, *Y*). Its counterpart has been found by the writer in other specimens. The vestige is interesting in this case because it indicates that the base of the adrenolumbar is a persistent portion of the "renal collar," and thus equivalent to the base of the left renal vein of a normal animal.

The bifurcation of the aorta, and the respective points of entry of the right external iliac vein and the left iliolumbar, into the post-caval, are situated the length of a segment cranial to their usual site, perhaps owing to the growth of the metanephros in its unaccustomed position below them. This has resulted in the union of the right ovarian (or reno-genital) vein with the external iliac; and also in the union of the left reno-genital with the iliolumbar vein[2]. The two latter vessels thus reach the post-caval *via* the same transverse connection. This connection appears to be a derivative of the iliac anastomosis between the two post-cardinals, for it lies dorsal to the common iliac arteries, ventral to the median sacral artery, and is continuous on its caudal side with the median common iliac vein, which is formed in the rabbit by the fused ends of the post-cardinals. The anastomosis seems to have been cranially displaced, like the aortic bifurcation. It usually lies well caudal to the left ovarian vein, which normally therefore, in crossing the mid-line, makes use of an entirely different anastomosis, namely, part of the dorsal aortic plexus of Strong (18).

[1] Reagan (17) regards this arrangement as normal for male rabbits, but appears to overlook its existence as a common variation in females.

[2] The iliolumbar vein of the rabbit lies ventral to the psoas muscle and is not homologous with the vein of that name in Man.

Perhaps because their small dimensions make them difficult to study, parts of the sympathetic nervous system of the normal rabbit, especially in the caudal region, are not well known. Most of these nerves are invisible in the fresh state, and even when preserved can only be dissected with the aid of a lens. Pending the completion of work now being undertaken on the typical morphology of this system, only a few remarks need be made regarding its structure in the anomalous specimen. Superficial appearances, at least, suggest that most of the fibres of *N* 4, travelling from the superior mesenteric ganglia, pass straight through the small ganglion near the ovarian artery, and are directly continuous with the fibres of *N* 3. The latter follows renal artery *A* 3*b* into the left kidney. *N* 1, running the length of the abdomen, takes an almost direct course from the superior mesenteric ganglia, to pass, *via* the renal artery *A* 1, into the right kidney. Thus both the kidneys (or their arteries) appear to be supplied by nerve fibres from the superior mesenteric ganglia. These ganglia are closely connected with the renal network in the normal animal: it is striking that the same association should appear to be maintained in the anomalous specimen, in spite of the long distance intervening there between the ganglia and the kidneys. It rather suggests that the functional destiny of fibres growing from a given source is not affected by ectopia of the organs. It is also interesting in connection with the findings of Uchida (19), to the effect that elements of the sympathetic system enter the kidney almost directly it is laid down, and certainly before it has migrated. They are distinguishable, for example, in a 9 mm. pig.

SUMMARY

A rabbit is described with coalesced kidneys, the right lying caudal to the left, and the two forming a solitary kidney-shaped body in an almost median position, far caudal to the normal site.

It is suggested that a factor, such as hypertrophy of the Wolffian bodies, the right more than the left, hindered the early stages of migration of the kidneys, so that they were arrested in the region between the umbilical arteries. Evidence is adduced that their fusion took place in this situation at the end of the 13th day of embryonic life, and was probably due to lateral pressure of the arteries on the growing blastemata. This and other examples suggest that once fused, if lying more or less medianly, kidneys are unable to migrate further on account of the obstruction afforded by the mesentery and the inferior mesenteric artery.

There are many anomalies in the vascular system. The four renal arteries arise from the iliacs, and from the bifurcation of the aorta. The main renal veins are joined to the corresponding ovarians, and these flow into the right external iliac and the left iliolumbar vein respectively. Embryological explanations are afforded for these relationships.

Following the arteries into the kidneys are three sympathetic nerves, mainly connected with the superior mesenteric ganglia.

It is pointed out that the normal asymmetrical positions of the kidneys in the rabbit, the left lying more caudally than the right, are probably due to the left-handed spiral twist of the caudal part of the embryo during the end of the second week.

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ANATOMICAL NOTES

ABNORMALITY OF SUBCLAVIAN ARTERY ASSOCIATED WITH PRESENCE OF THE SCALENUS MINIMUS

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Much has been written about the vascular symptoms of cervical rib. While in most cases these are due to pressure of the sympathetic fibres contained in the lowest trunk of the brachial plexus against the abnormal rib (Stopford (13)), in other cases they are due to direct pressure on the wall of the subclavian artery, sometimes with the production of dilatation or even aneurism beyond the constricting point. (Halstead (5), Moore (7), Billington (2), Murphy (9), and, later, Adson and Coffey (1), laid stress on the action of the scalenus anterior in compressing the artery against the rib; indeed, Adson relieved symptoms in several cases simply by dividing the scalenus anterior tendon.)

But I have seen no account of arterial obstruction due to the muscular action of the scalenus anterior in the absence of a cervical rib, nor have I heard of a case where the dilatation occurred proximal to the constricting point. I think, therefore, that the following case, which was discovered in the cadaver, is worthy of record.

The subject was a male, aged 43, a Russian. There was nothing in the clinical history to suggest an anomaly of the subclavian artery. The Wassermann test had not been carried out.

The innominate artery was dilated in a fusiform manner and the dilatation extended into the first part of the subclavian but did not affect the right common carotid. The innominate artery was also elongated and bent in an S-shaped manner, the first half being convex above and to the left, and the second half convex below and to the right. There was a marked narrowing of the second part of the subclavian artery, which was highly arched and elevated above the first rib. This part of the artery was separated from the lowest trunk of the brachial plexus by a slip of muscle, the scalenus minimus, which arose from the transverse process of the 7th cervical vertebra close to its root and was inserted into the pleura, and into the first rib behind and in continuity with the scalenus anterior. The scalenus anterior received an additional attachment to the 7th cervical vertebra in common with the scalenus minimus.

The left subclavian artery was normal. The scalene muscles were disposed in a similar fashion on the left side. There was no cervical rib on either side. There was a deviation of the thorax to the left side of the median plane.

Scalenus minimus muscle

No mention of this muscle is made in Cunningham's (3) or Gray's *Anatomy* (4), but it is described in Quain's (10) and Morris' *Anatomy* (8), and in *Spalteholz Handatlas* (12) as scalenus minimus (B.N.A.); by Testut (15) as scalenus intermedius; by Le Double (6) as scalenus pleuralis. A sketch showing the muscle is given in an article by Shore (11). Todd (16) gives illustrations showing the relations of the scalenus minimus to the subclavian artery and brachial plexus. Either the artery or the nerve may be raised above the first rib; the right artery is usually at a higher level than the left. Stott (14) found that when the insertion was close to or incorporated with that of the scalenus anterior, the subclavian artery was elevated from the upper surface of the rib, and that the sulcus subclaviae was occupied by the lowest trunk of the brachial plexus.

Among fifteen dissecting-room subjects I found the scalenus minimus present on both sides in four cases; on the right side only in two cases; and absent in the others; i.e. present ten times out of thirty (33 per cent.). In one foetus examined it was bilateral. These findings confirm those of Stott and Zuckerkandl (quoted in Morris' *Anatomy*).

In Cunningham's *Anatomy* the statement is made that the subclavian artery may pierce the scalenus anterior. It may be that in such cases a scalenus minimus was present, but was regarded as a part of the scalenus anterior.

I noticed that in a few cases the upper attachment of the scalenus anterior to the 6th transverse process extended laterally on to the posterior tubercle, so that the 7th cervical nerve pierced the muscle instead of emerging from behind it, and in one case the slip to the 5th transverse process also extended laterally. In no other case besides the one which presents the anomaly of the subclavian artery did I find the scalenus anterior attached to the 7th cervical vertebra.

Summary

A case is described of a narrowing of the second part of the right subclavian artery, with a fusiform and sinuous dilatation proximal to that narrowing. It is suggested that the cause is an elevation and compression of the artery by slips of muscle which descend from the 7th cervical transverse process to the scalene tubercle of the first rib. The posterior slip occurs frequently as a separate muscle, the scalenus minimus. A slip of the scalenus anterior attached to the 7th cervical vertebra is, however, uncommon. The fact that no cervical rib was present lends support to those who stress the part played by the scalenus anterior where symptoms are associated with the presence of cervical rib.

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STAINING OF NERVOUS TISSUE IN BULK FOR HISTOLOGICAL INVESTIGATION FOR CLASS PURPOSES

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A considerable saving of time and of labour can be achieved by staining in bulk material that is destined for class-teaching purposes. It is hardly necessary to emphasise that this method is not suitable for the more precise investigations demanded by research work, nevertheless constant and reliable results can be obtained by due attention to detail. Methods have been already published (1) that involve staining in bulk with haematoxylin and eosin, and with orcein, together with a picrocarmine method for nervous tissues. Staining in bulk for the central nervous system is particularly useful, especially for paraffin sectioning, in that it minimises the stages at which disintegration of sections is prone to occur: for celloidin work the sections are best stained separately.

The following three methods give uniformly good results with the central nervous system, provided that the material used is *fresh*.

I. *Picrocarmine method*

(The original method has been somewhat modified)

Fresh material (whole brain) is put straight into 7 per cent. formalin made up in physiological NaCl solution, and left therein with one or two changes for one week. It is a good plan to tie the brain up in coarse butter muslin until it is fixed on the outside. After a week the brain is usually firm enough to slice with a razor: if the brain stem only is being used an ordinary flat-sided razor is quite suitable: if the whole brain is being used then sectioning is best carried out with an ordinary bacon slicer as described by Green (2). The blocks should be *not more* than $\frac{1}{2}$ cm. thick. These slices are transferred to Müller's fluid for about 6 weeks: during this time the fluid should be changed several times, and the blocks should not be allowed to rest on one another or on the bottom of the vessel. When fixation is complete the blocks are transferred without washing to Stöhr's picrocarmine (3). (A crystal of thymol should be added to the filtrate, instead of the recommended chloroform.) After 1 or 2 days the staining fluid is poured off, the blocks and container rinsed with water to remove all sediment, and then the blocks are put into fresh staining fluid and left there for *at least* a month. It is almost impossible to overstain. It is a good plan to add to the blocks being stained one or two pieces of unwanted cerebral cortex from the same brain that have been treated in the same way, and then these can be cut through at intervals to see whether the stain has penetrated right through the piece.

The blocks are then taken up through the alcohols in the usual way, picric acid being added to the alcohol to prevent removal of the stain. The material is then cleared in picroxylol, and imbedded as usual in paraffin wax. Sections should be about 30μ thick.

II. *Aniline blue-black method*

The preliminary fixation in formalin, followed by sectioning and after-treatment with Müller's fluid for about 6 weeks, is carried out as above. The blocks are then

washed quickly in tap water, then in distilled water, and transferred to the stain. The staining mixture consists of

Aniline blue-black	2 gm.
Distilled water	60 c.c.
Alcohol (97 per cent.)	40 c.c.

and the secret of the staining lies in using a really reliable aniline blue-black which is soluble in water (such as Gurr's). Staining can be accelerated by putting the blocks into the incubator at 37° C.: in this case thin blocks ($\frac{1}{4}$ cm.) are well stained in 11 days. For thicker blocks more uniform staining is obtained by staining for about 3 weeks at room temperature: as before, the penetration of the stain can be gauged by using some control blocks.

After staining, the pieces are washed quickly in water, and transferred to 50 per cent. alcohol: they are then taken up through the alcohols, dehydrated, cleared in xylol, and imbedded in paraffin wax in the usual way.

For these two methods of staining mordanting in chrome salts is essential.

III. *Ranson's silver method*

The application of this method has been already described (4). In brief, formalin fixed material is cut into slices of suitable thickness (2–3 mm.), thoroughly washed for 24 hours in running tap water, and treated by the standard pyridine-silver method of Ranson. Sections should be about 10μ thick.

In sections from blocks stained by these three methods, the distinction between the grey matter and the fibre tracts is perhaps best seen in those stained by picro-carmine or aniline blue-black: the actual detail of nerve cells and their processes is best seen in the silver preparations.

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REVIEWS

Bone Growth in Health and Disease. By H. A. HARRIS, D.Sc. (Lond.), M.B., B.S. (Lond.), M.R.C.P., Professor of Clinical Anatomy, University College and University College Hospital, London. (London: Oxford University Press.) 1933. Pp. xv + 248, 201 figs. Price 34*s.* net.

"This little book," writes the author in his preface, "is an account of the clinical and experimental researches on the growth of bone which I have pursued from a coign of vantage as liaison officer between University College Hospital, London, on the one hand and the Institute of Anatomy and Embryology at University College on the other." Prof. Harris has availed himself to the full of all the opportunities which his professional office has provided him with for studying the behaviour of living bone and produced a work of outstanding originality.

In describing it as "this little book," however, he has been blinded by his modesty; in no sense is the book a "little" one. The publishers show a more just appreciation of the work by the price they attach to it—34*s.* Nor is the price excessive when the number and excellence of the illustrations are kept in mind. Still we wish the work could have been produced at a cost which would have permitted every student of medicine to be the owner of a copy.

When Prof. Harris came to put together the experimental results he had obtained and the clinical observations he had made on bone-growth, two ways were open to him. He could have brought together the various studies on the growth of bones which have been made and published in the present century, added his own observations and thus given us a systematic treatise, or he could have made his own observations the theme of his text and incidentally have alluded to the work of others. Prof. Harris chose the latter way and has thus given us a work in which his personality finds a warm reflection. And, as the readers of this *Journal* know, Prof. Harris is a philosopher as well as an anatomist and in these pages he is philosopher and anatomist. He has also taken the opportunity of laying before his readers evidence relating to problems with which his name is already associated. Amongst these may be mentioned the problem relating to the origin and nature of the "transverse lines" of long bones, the growth of cartilage—particularly of cartilage covering articular surfaces, the fate of cartilage cells at lines of ossification—particularly the part played by these cells in bringing about calcification of cartilage. Prof. Harris discovered that cartilage cells, as they approach the line of ossification, contain glycogen. He inferred that this ought to be the case if the ferment "phosphatase" arose and acted in the manner attributed to it by its discoverer Dr Robison. He searched and found that it was so.

Prof. Harris has divided his book into three parts. In Part I an excellent skiagraphic and experimental study is given of the transverse lines which cross the shafts of long bones. The author traces these to periods of arrested growth caused by illness or nutritious disturbance in childhood or youth. He compares such lines to those to be seen in teeth, nails, fish scales and trees—all being the result of delayed growth.

Part II is an account of the normal growth of bones and of the changes in rachitic bones. The author's studies of the calcification which precedes ossification in cartilages and of the differences in the growth of cartilage at the different epiphyses are worthy of careful study. It is doubtful, however, if his designation of cartilage as a "vegetative" tissue and his likening it to tumour tissue will bear close examination. His tacit acceptance of the "archusia-ergusia" hypothesis of Burrows does nothing to clarify the subject. In the ossification of calcified cartilage, Prof. Harris thinks that some of the senescent cartilage cells survive and are rejuvenated to form osteoblasts.

This view will not meet with wide acceptance, and the evidence advanced in this book is insufficient to sustain it. Prof. Harris also embraces Kölliker's view that bone absorption and remodelling is effected largely by the activity of osteoblasts, a conception which is at least debatable. The account of the pathology of rickets and the correlation of this with skiagraphic appearances are admirable.

Part III discusses the significance of the processes of bone growth in diseases of the skeleton. The study of mitotic activity in growing epiphyseal cartilage is of much interest. The view that synovial fluid is produced by mechanical wear and tear of the articular cartilages and is absorbed by the synovial membrane, although a good working hypothesis, is not supported here by any tangible evidence. The inclusion of a section on senescent changes in the placenta seems scarcely appropriate. A final section, discussing the significance of glycogen and phosphatase in the biochemistry of bone growth and urging that the biochemical viewpoint is essential to the student of bone pathology, contains valuable suggestions; but perhaps too little is said of the influence of the parathyroid hormone on the metabolism of bone.

There is not a page without its challenge—often thrown out, we suspect, provocatively rather than with the expectation of serious acceptance. Were the critic to give full expression to all the points in which Prof. Harris seems to him to stand in need of correction, or at least of amplification, this review would go beyond reasonable bounds, but there is one important statement which should be challenged now. It relates to Achondroplasia. The specimen represented in Fig. 123, p. 152, is described as a typical case of achondroplasia. The reviewer would describe it as a typical cretin and the description given by Prof. Harris of the microscopic structure of the "epiphyseal line" is in keeping with this cretinoid diagnosis and altogether against his diagnosis of achondroplasia.

Nevertheless, Prof. Harris has produced a valuable and stimulating work, which should be in the hands of every student of the pathology and skiagraphy of the skeleton.

Additional Note

Since the above was written Prof. Harris has submitted sections of the thyroid gland of the full-time foetus shown in Fig. 123 of his book. The reviewers agree with him that the gland possesses none of the features which characterise the thyroid of a cretin. Nevertheless one of the reviewers (A. K.) holds that the foetus shown in Fig. 123 differs from the condition usually called achondroplasia in external appearance and in the structure revealed in the section of the femur (Fig. 125).

The Action of the Living Cell. Experimental Researches in Biology. By Fenton B. Tuck. (New York: The Macmillan Co.) 1933. Pp. x + 308, 17 figs. Price $3.50.

In this volume the author develops fully his conception founded on observation, his own experiments, and general reading that an appropriate stimulus causes cells to yield an endocellular component which is capable of both exciting and depressing the activities of neighbouring cells. This endocellular component he has named "cytost."

Beyond the statement that it is thermostable nothing is known about the chemical identity of this substance. Its formation arises during tissue cytolysis. Although a small amount of it in the tissues is not harmful, is perhaps even beneficial, yet any untoward accumulation of it will produce pathological changes. The erosion of the mucous membranes of the uterus by the fertilised ovum produces tissue autolysis, cytost and the toxaemias of pregnancy. During wilful activity or enforced quiescence the conditions are favourable for the production of cytost. It comes into existence

during starvation, semi-starvation and dietetic deficiency. It affects cell multiplication, reproduction, egg-laying and the like. It explains shock, the general effects of burns and the same substance plays its part in producing senescent changes. Its effects in the animal world can be paralleled in plants. A medley of evidence, good, bad and doubtful, lies behind these statements.

Whatever validity may reside in the author's thesis it is so diluted by his enthusiastic expansion of it that in the end it loses all interest.

The Anatomy of the Eye and Orbit. By EUGENE WOLFF, M.B., B.S. (Lond.), F.R.C.S. (Eng.). (London: H. K. Lewis and Co., Ltd.) 1933. Cr. 4to. Pp. viii + 310, 173 figs. Price 31*s.* 6*d.* net.

This book deals most comprehensively with the anatomy not only of the eye and orbit but also of the orbital adnexa, and with the central connections, development and comparative anatomy of the visual apparatus. A special chapter describes the normal appearances seen with the slit-lamp, without entering into the technique of this method of examination. The anatomical standard is high, and how remarkably evenly this standard is maintained throughout all sections is one of the chief impressions formed on reading through the book. Only once was a little disappointment felt, that the central connections of the oculomotor nerve had not been given fuller consideration. Extensive bibliographical lists at the ends of the chapters add to the usefulness of the work as a book of reference. These lists seem to be very well chosen and are noticeably up-to-date. The simple, direct style of the text is attractive. In addition to short sections of practical considerations, there are scattered throughout the text terse sentences in italics which point a clinical or pathological moral and vivify the tale.

The illustrations are a prominent feature of the book and deserve great praise. A pleasingly large proportion are original; they are unusually and most commendably big, and they are beautifully reproduced. The topographical pictures by A. K. Maxwell of the orbit and adjacent parts, including parts of the brain, are among the finest we have seen.

Altogether this is a book upon which author and publishers are to be warmly congratulated.

Lymphatics, Lymph and Tissue Fluid. By CECIL H. DRINKER, B.S., M.D., Professor of Physiology, Harvard School of Public Health, and MADELEINE E. FIELD, D.B., PH.D., Instructor in Physiology, Harvard School of Public Health. (London: Baillière, Tindall and Cox.) 1933. Pp. xvi + 254, 14 figs. Price 17*s.* 6*d.* net.

This monograph on lymphatics and their functions contains a short introduction, one hundred and eighty-nine pages of text divided into eight chapters, a few illustrations, a number of tables, about five hundred references and an adequate index.

The first chapter pays a handsome tribute to the work of anatomists in establishing the structure of lymphatics, and the authors accept their statements that the lymphatics are an offshoot of the venous system permeating the greater part of the body, having nothing to do with coelomic spaces, bursae, or joints, furnished with their own specific endothelium and forming a closed system.

Matter of microscopic dimensions may enter lymphatics in various ways, but the authors believe that permeability of the endothelium, aided by changes in pressure and motion, is the most important.

Chapter III turns to the permeability of blood capillaries. The endothelium of these is permeable to proteins, especially albumin. The degree of permeability is greater at

the venous end of the capillary and this varies in different parts of the body. Starling first formulated the principle that filtration from the capillaries would be a balance between the osmotic pressure of the blood proteins and the capillary blood pressure. To this main statement a number of subsidiary factors, some of an anatomical kind, must be added.

In Chapter VI the results of the investigation of the composition of lymph from chemical, physical and cellular standpoints are collated. A dog in 24 hours pours into the blood stream 3,300,000,000 lymphocytes. The authors suggest that the constancy of the number in the blood depends not so much on formation, destruction or transformation but rather on the circumstance that the lymphocytes for the most part pass from the blood to the tissues and then back to the lymphatic and so again to the blood. Composition of the tissue fluid is substantially the same as that of lymph.

The authors' views of the functions of lymphatics are shown by the following quotation: "The filtrate from the blood capillaries to the tissue spaces contains water, salts and sugar in the concentrations found in the blood, together with serum globulin, serum albumin and fibrinogen in low concentration, lower probably than that of tissue fluid or lymph; that water and salts are reabsorbed by the blood vessels and the protein enters the lymphatics together with water and salts in the concentration existing in the tissue fluid at the moment of lymphatic entrance."

The final chapter deals with the practical applications of these conceptions.

The Coming of Man: Was it Accident or Design? By ROBERT BROOM, F.R.S. (London: H. F. and G. Witherby.) 1933. Pp. 234, 35 figs. Price 10*s.* 6*d.* net.

The author of this book, with the arresting sub-title, is distinguished for his contributions to the comparative anatomy of the Mammalia and in particular for his work on the Mammal-like Reptiles. In this volume he passes in review his life-work and reflects on the sad inadequacy of all the proposed theories of evolution and finds comfort only in supposing that some mysterious force is behind the whole pageant of life urging it onwards.

He discusses in considerable detail the evolution of the Primates and devotes a large section of the book to *Australopithecus*, whose importance he feels has not yet been assessed at its true value. *Australopithecus*, with its long skull, well-developed frontal brain areas, and increased cerebral volume, stands close to the common ancestor of Man and the Anthropoids and is the most man-like of all the great apes. From the materials found in the deposits associated with the skull the author deduces that this fossil ape might have known the use of weapons and with these perhaps pursued and slew its prey.

The Study of Anatomy. 2nd edit. By S. E. WHITNALL, M.A., M.D. (London: Edward Arnold.) 1933. Pp. 93. Price 4*s.* net.

Prof. S. E. Whitnall's brochure on *The Study of Anatomy*, a second rewritten and enlarged edition of which has recently been published, should be in the hands of every medical student commencing the study of the subject. In it will be found invaluable advice presented in an eminently readable form. The professor obviously knows how to captivate his student and further knows how to arouse his interest and enthusiasm. Should the advice given be followed the dead bones will live and the complex mechanism of the human body will prove a most attractive study. Emphasis is laid upon the importance of visualising and not merely memorising, of studying the body at the expense of the book and avoiding the converse, and of the greater profit to be derived by acquiring main facts instead of concentrating on details. The author is not content with the learning of anatomy only but gives further good advice

on examinations, on the importance of maintaining *mens sana in corpore sano*, and, last, but by no means least, on the educational and recreative value of general reading.

Laboratory Atlas of the 13 *mm. Pig Embryo* (*Prefaced by younger stages of the Chick Embryo*). By E. A. Boyden. (The Wister Institute Press.) 1933. Pp. iii + 91. Price $2.

This useful atlas, prepared by Prof. Boyden of the University of Minnesota, provides a concise guide to the medical student who wishes to gain that measure of knowledge of embryology which will be of help in his clinical work. The book serves as a rapid and thorough introduction to mammalian organogeny.

The earlier stages of embryology are covered by a series of drawings of the chick and duck embryo at the 36- and 48-hour stage. The main mass of the atlas consists of line drawings of sections of the 13 mm. pig embryo arranged in such a manner that the development of the organs of the various systems can be pursued in orderly fashion. Several drawings of the valuable models prepared in the Harvard Medical School make the interpretation of the transverse sections easy even to the student who has but a poor notion of three-dimensional anatomy. A good student provided with serial sections of the pig or human embryo of approximately this stage could obtain valuable first-hand acquaintance with the essentials of organogeny and teratology in the course of ten or twelve half-days. The outline drawings in themselves save valuable time to the student.

ON THE MECHANISM CONTROLLING THE GROWTH IN LENGTH OF THE LONG BONES

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It has been well known, since the classical experiments of John Hunter (1) in 1794, that the growth in length of the long bones occurs only at the junction cartilages. These structures are especially adapted for the process of endochondral ossification leading to the apposition of new bone in a certain direction. It seems also that the normal function of these growth cartilages is dependent upon the pituitary growth hormone. The latter, however, is a general growth stimulus and as such dependent again on the junction cartilage for the determination of the direction of the growth.

The generally accepted conception is that the junction cartilages are highly specialized structures, formed during foetal life, and that therefore the growth of the long bones in length is only possible as long as derivatives of the original junction cartilage anlage are present. This conception has been substantiated by the observations in human subjects and in animals that experimental or pathological destruction of the epiphyseal cartilages stops the growth in length of the injured bone for ever.

The high degree of specialization of these structures as compared with other types of cartilage is not only suggested by their singular histological appearance, and by the observation mentioned above, but also by transplantation experiments, which show that their structure and appearance is not changed if their relation to the shaft of the bone is altered. Thus Helferich (2) and later Rehn and Wakabayashi (3) showed that autoplastic transplants of the epiphyseal cartilage continue to form new bone if the graft takes. Still more interesting in this respect are the experiments of Brücke (4) who reimplanted the junction cartilage of the ulna and radius in rabbits after rotating them through 180 degrees. He found that after this operation bone apposition took place only on the side originally facing the diaphysis, so that the epiphyses became greatly elongated. Thus the orientation of the cartilage columns was not changed.

Experiments performed in this laboratory lead us to believe that during the first weeks of life the autonomy of the bone, in so far as the determination of its growth in length is concerned, is much greater than has been suspected. It seems to us that the growth of very young bones is largely independent both of the pituitary growth hormone and of the derivates of the epiphyseal cartilage anlage. We have already published our experiments on the first point, showing that rats hypophysectomized at the age of 21–24 days may continue to grow

for several weeks (5). In the present paper we intend to report our observation that even removal of the original anlage of the epiphyseal cartilage does not necessarily stop the growth in length of immature bones.

Twenty-five rats, 12–15 days of age, were used. In fifteen of them the right leg was amputated, with transverse section, above the junction cartilage of the femur, so that the entire growth-zone was removed. The animals were killed at intervals and the amputation stumps examined histologically. A few days after operation the end of the stump was closed by proliferating spindle cells showing all the morphological characteristics of osteoblasts. Somewhat later, after 8–11 days, these osteoblasts begin to transform into chondroblasts and

Fig. 1. Amputation stump 8 days after operation; in the lower part of the field is the marrow cavity; above this a layer of irregular trabeculae can be seen, while the top part of the field shows numerous osteoblasts and chondroblasts, with a small cartilage islet in the centre.

more or less irregularly arranged islets of cartilage appear around the bone strings (see fig. 1). Still later, after 19–25 days, the end of the bone is closed by a regular layer of cartilage, the proximal part of which shows the typical structure of the growth-zone (see fig. 2). Measurements of the length of the femur stump at operation and at autopsy show that this cartilage leads to very active growth in length.

In a second series, 10 rats 14 days of age were used. The experiment was performed under the same conditions as the previous one, but the femur was amputated with an oblique section. The result was that numerous osteoclasts formed on the pointed end of the stump and led to its rapid resorption. The bone did not grow in length until the processes of transformation on the stump made the end of the bone exactly perpendicular to the length axis of the shaft.

Then a growth cartilage formed—in very much the same way as in the previous series—and the growth in length was resumed (see fig. 3). Similar experiments on rats more than 5 months of age have never been successful. These results may be compared with Child's demonstration that diagonal slices from Planarian worms retain their original axis in regeneration.

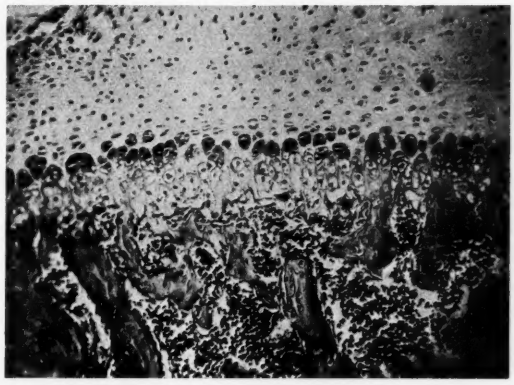

Fig. 2. Amputation stump 19 days after operation, showing newly formed typical growth cartilage line.

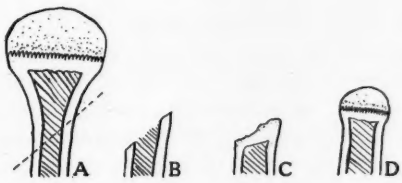

Fig. 3. Diagram showing formation of new junction cartilage line on an obliquely cut amputation stump.

A. Normal bone; broken line indicates plane of amputation.

B. Stump immediately after amputation.

C. Beginning reconstruction of the stump.

D. The amputation stump with newly formed, regular growth-zone, developed in the same plane as the epiphyseal cartilage which has been removed from the original bone.

These experiments show that in early post-foetal life the long bones are to a great extent autonomic in their growth and probably much more under the controlling influence of formative centres situated within themselves than in later stages of development. The young animal's independence of endocrine control may perhaps be regarded as an instance of phylogenetic recapitulation (6).

SUMMARY

If the distal end of the femur is removed in rats during the first few weeks of life a new growth cartilage is formed and the growth in length is resumed.

This new growth cartilage forms always in a plane at right angles to the long axis of the shaft, quite irrespective of the plane of amputation.

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THE INNERVATION OF THE EXTRINSIC OCULAR MUSCLES[1]

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INTRODUCTION

This investigation was undertaken at the suggestion of Prof. G. Elliot Smith with the object of studying the deep origin of the proprioceptive fibres in the nerves of the eye muscles. It is generally believed that the afferent fibres of these muscles come from the fifth nerve, but there is still disagreement as to whether the cells of origin of these fibres lie in the Gasserian ganglion, in the mesencephalic nucleus of the fifth nerve, or in some other nucleus inside the brain. Although afferent fibres are known to be present in the oculomotor, trochlear and abducens nerves, their points of entrance into these nerves are still unknown.

In this paper an attempt is made to study histologically the relation between the mesencephalic root of the trigeminal and the motor nerves of the eye, and to trace by degeneration methods the course taken by these afferent fibres to reach their destination.

I wish to express my best thanks to Prof. G. Elliot Smith, under whose supervision this work has been carried out, to Dr U. Fielding for her invaluable guidance and criticism, and to Prof. J. P. Hill, in whose department the work has been done, for his kind interest and advice. I am much indebted to Sir Charles Sherrington and to Dr H. M. Carleton for their kindness in allowing me to do the operations in the Physiological Department at Oxford. The microphotographs are the skilful work of Mr F. Pittock, to whom my best thanks are also due.

PREVIOUS WORK

Meynert (1867) was the first to associate the mesencephalic root with the fifth nerve and to recognise the sensory character of its cells. He referred to the close relationship existing between the central path of the fourth nerve and the mesencephalic root, but described no connection between them. Since then, the mesencephalic root has been extensively studied by several authors. Their opinions differ, however, on the nature of its function as well as on the peripheral distribution of its fibres. While the morphological character of its cells favours a sensory function, the fact that in most animals the root leaves the brain with the motor fibres of the fifth nerve has suggested a motor one.

[1] Portion of thesis approved for the degree of Ph.D. in the University of London.

Merkel (1874) assumed the mesencephalic root to be a trophic centre; while Huguenin (1873) suggested a vasomotor function.

Golgi (1893), Van Gehuchten (1895), Kölliker (1896), and Ramon y Cajal (1895, 1908) are among those who believed it to be motor in function.

Points in favour of a motor function of the mesencephalic root are the situation of its cells inside the brain, the incorporation of its fibres with those of the motor root of the fifth nerve, and the peripheral distribution of these fibres in muscles.

Among the authors who regarded the mesencephalic root as sensory are Meynert (1867), Johnston (1909), Willems (1911), Kosaka (1912), Allen (1919) and Weinberg (1928). The main points held in favour of a sensory function of that nucleus are:

(1) The striking resemblance in shape between the cells of the mesencephalic root and the ganglion cells of the spinal roots.

(2) The dorsal situation of the mesencephalic cells in the brain stem and their derivation from the alar lamina.

(3) The interesting finding of Ambronn and Held (1896) that the fibres of the mesencephalic root become myelinated at a different time from the fibres of the motor root of the fifth nerve.

Concerning the relationship of the mesencephalic root to the eye muscles, May and Horsley (1910) found that intracerebral section of the mesencephalic root causes no degeneration in the ocular nerves. Degenerated fibres were only seen in the fourth nerve, but this was always due to damage to that nerve in the course of the operation on the mesencephalon. They concluded that the mesencephalic root is not connected with the innervation of the ocular muscles. It is of interest to note here that May and Horsley failed to demonstrate, with the Marchi method, any degeneration in the branches of the trigeminal peripheral to the ganglion in animals in which intracerebral section of the mesencephalic root was done. They therefore suggested that the mesencephalic root or some of its fibres end in the Gasserian ganglion.

Sherrington (1897, 1898), experimenting on the cat and monkey, found, after cutting the third nerve at its origin from the brain, that all the myelinated fibres in the muscles supplied by this nerve were degenerated, except for a few fine ones which he thought probably arose in the ciliary ganglion. The same picture was seen in the external rectus muscle after cutting through the ophthalmic division of the fifth nerve and the sixth nerve. He concluded that the ophthalmic division of the fifth nerve does not supply the sensory fibres to those muscles. Furthermore, Sherrington found that no obvious impairment in the movements of the eye-ball resulted after section of both trigeminal nerves in the monkey, and that the combined section of both trigeminal and both optic nerves "even after section of the encephalic bulb" did not considerably depress the tone of the extrinsic muscles of the eye. The tone of these muscles is therefore not dependent on trigeminus or opticus but may be referable to afferents continued within the third, fourth and sixth

nerves themselves. These observations were confirmed and extended by Tozer and Sherrington (1910), who found that the fifth nerve may send a few fibres to the eye muscles; the number of these in the cat, rabbit and monkey is insignificant. The third, fourth and sixth nerves are afferent-efferent: their afferents are exclusively proprioceptive.

Willems (1911) was the first to prove the proprioceptive function of the mesencephalic root for the muscles of mastication. He found that, in the rabbit, all the muscles supplied by the fifth nerve were centrally localised in the main motor nucleus. On the other hand, most of these muscles were also represented in the mesencephalic nucleus. Fibres from the latter nucleus to the masticatory muscles were regarded by Willems as proprioceptors. Whereas avulsion of the muscular branches of the mandibular nerve would result in degeneration of nearly all the cells of the motor nucleus, chromatolysis in the mesencephalic root involves only 815 cells out of a total number of 1590. From this, one is justified in concluding that only 51 per cent. of the mesencephalic cells contribute fibres to the mandibular nerve. But Willems did not feel justified in hazarding such a conclusion; he states that this was due to unsuccessful experimentation and referred the matter for further inquiry.

McLean (1926) reported that, in the dog and cat, the cells of the nuclei of the third, fourth and sixth nerves may be separated, according to their size, into two distinct types, small and large. From a consideration of "experiments with degeneration" the author expresses the opinion that the smaller cells in the central motor nuclei of these nerves may possibly be concerned with the kinaesthetic sense of the extrinsic muscles of the eye.

Freeman (1925, 1927), after removal of the whole of the orbital contents in four cats, found that the mesencephalic root on the operated side and at the level of the oculomotor nucleus was slightly degenerated. On the opposite side, degeneration of the same root was found to be at the level of the nucleus of the fourth. Freeman assumed that the mesencephalic root supplies the proprioceptive fibres not only to the muscles of mastication, but also to the extra-ocular muscles.

Woollard (1931), after section of the oculomotor nerve in one rabbit, found chromatolysis of the mesencephalic cells on the side of the operation, but the mesencephalic root on the opposite side was quite normal. He concluded that the finer nerve fibres seen in the ocular muscles, and regarded by him as sensory, have their origin in the mesencephalic root of the fifth.

METHODS

Cats were used throughout this investigation. The oculomotor or the trochlear nerve was cut at its exit from the brain and before any possible communication from the fifth. The mid-brain was sectioned serially in transverse, sagittal, horizontal and oblique directions, and the mesencephalic root and the related structures were examined histologically.

Section of the oculomotor nerve was performed in one stage, the skull

being trephined on one side only. This was found to be much more convenient than the two stages operation used by Hines (1931). The animal was anaesthetised with an intraperitoneal injection of nembutal (30–40 mg. per kg. body weight). The skin, fascia and muscle, on the side to be operated upon, were divided and dissected away from the bone of the temporal fossa. The skull was trephined and the trephine hole enlarged into a big triangular or oval opening. The brain was lifted on a smooth spatula which was then gently moved farther until the edge of the tentorium cerebelli became visible. The third nerve appeared as a white cord medial to the crus cerebri, while the fourth nerve was seen lateral to the crus and somewhat caudally. Either nerve could then be easily severed.

The silver technique (modified from Sand, 1911) was applied to all the material used. Paraffin sections cut at 15 μ thickness were mounted and then left in 10 per cent. solution of silver nitrate for 48 hours. The time of the silver bath is by no means constant. Some of the sections were impregnated in a shorter time, while others required a much longer period. As to the exact time required for complete impregnation, only practice with the method will show when the sections are adequately tinted. On removal from the silver bath, the sections were rinsed in distilled water for a few seconds and then reduced for 5 minutes in the following mixture:

Tannic acid	...	3·0 gm.
Gallic acid	...	5·0 ,,
Sodium acetate	...	10·0 ,,
Distilled water	...	1000·0 c.c.

They were then washed in distilled water, toned with gold and fixed in sodium hyposulphite; lastly they were dehydrated, cleared and mounted in canada balsam.

DEGENERATION EXPERIMENTS

The ocular muscles, in contrast to all other muscles, receive a nerve supply which is strikingly rich. The size of a nerve relative to the bulk of its muscle, the repeated division of its fibres and the frequency with which we see its endings are all outstanding features in the innervation of these muscles. An ocular nerve, as soon as it enters the muscle, is seen to divide repeatedly as it proceeds towards the tendon. In a normal eye muscle preparation large branches of nerve are seen in the proximal part of the muscle. Farther distally these branches become smaller, partly as a result of division, partly because of the ending of some of their fibres. In this distal part of the muscle, nerve fibres are seen to run towards the tendon either singly or in groups of four to eight fibres. These fibres are usually thinner than those terminating in a motor end-plate. As pointed out by Sherrington, motor endings are usually seen in the fleshy part of the muscle up to about its middle; more distally they are rare. A motor fibre near its ending begins to thicken; its internodes become shorter. It crosses the muscle fibres transversely and may

then divide, and each division ends on a muscle fibre in a motor end-plate. Sensory endings are abundantly seen both in muscle and tendon, though at times it is difficult to decide whether a certain ending is motor or sensory, partly on account of their variant types and partly because of the difficulty in determining, in a longitudinally cut muscle, whether a nerve fibre is ending epilemmally or hypolemmally. Occasionally a sensory fibre, while proceeding distally, would reverse its course and proceed proximally to terminate on a muscle fibre in a brush-like manner (fig. 1). At the musculo-tendinous

Fig. 1. Fig. 2.

Fig. 1. Microphotograph of a nerve fibre reversing its course to proceed proximally in the muscle; the direction is indicated by the fact that the entering branches from the main nerve of supply are directed distally. Sherrington and Huber regard such recurrent fibres as sensory. × 176.

Fig. 2. Microphotograph showing the parallel arrangement of sensory fibres in the musculo-tendinous part of the eye muscle of cat. × 240.

junction, single nerve fibres run parallel to the tendon fibres and after branching dichotomously end epilemmally on the tendon fibres. Fig. 2 shows the parallel arrangement of the sensory fibres to the distal end of the muscle fibres.

Section of the oculomotor nerve was performed on six cats. The time allowed for degeneration was as follows: 7 days (one cat), 13 days (two cats), 21 days (one cat), and 27 days (two cats). The fourth nerve was cut in one cat; the degeneration time was 6 days.

In the cat sacrificed 7 days after the operation there was degeneration of all the thick fibres in the trunk of the third nerve distal to the point of

sectioning. Thinner fibres were only segmented transversely as they take a longer time to degenerate. In between these degenerating fibres there was a fair number of very minute myelinated ones which appeared quite healthy. The intramuscular branches of the nerve exhibited a similar appearance. No nerve endings were seen. The same result was observed in the superior oblique muscle of the cat in which the fourth nerve was cut.

In the other cats, degeneration of the nerve fibres was more complete. Nerve fibres running parallel to the muscle fibres and directed distally into the tendon were no longer seen. The few minute fibres that persisted were

Fig. 3. Microphotograph showing the connection of the ciliary ganglion with the third nerve—from a cat sacrificed 27 days after section of the oculomotor nerve. It will be noticed that nerve fibres from the cells of the ganglion are running into the third nerve. ×96.

in a completely sound condition and could be seen in most of the intramuscular branches of the nerve. Both motor and sensory endings have entirely disappeared. In one of the sections from the inferior rectus muscle of a cat killed 13 days after the operation a minute nerve fibre was seen to end on one of the muscle fibres, and in another a non-myelinated fibre, after bifurcation, could be traced to lie in very close relationship with the wall of an arteriole. In a cat sacrificed 27 days after the operation the ciliary ganglion was examined along with the branch from the third nerve to the medial rectus. It was noted that some of the cells of this ganglion cross the boundary of their territory and come to lie in the connection from the third nerve. Minute fibres from these cells run backwards into the oculomotor nerve (fig. 3).

HISTOLOGICAL STUDIES

The mesencephalic root

A detailed description of the mesencephalic root in the cat is not contemplated. This has been done by Johnston (1909), Thelander (1924), Weinberg (1928) and others. It is to be noted, however, that, although the cells of the mesencephalic nucleus may be seen as far cephalad as the posterior commissure, the fibres of the root were only seen to begin at some distance distal to the anterior limit of the nucleus. The root bundle is small and slender opposite the anterior part of the superior colliculus where it is made up of only a few fibres. As it proceeds caudally, the size of the root gradually

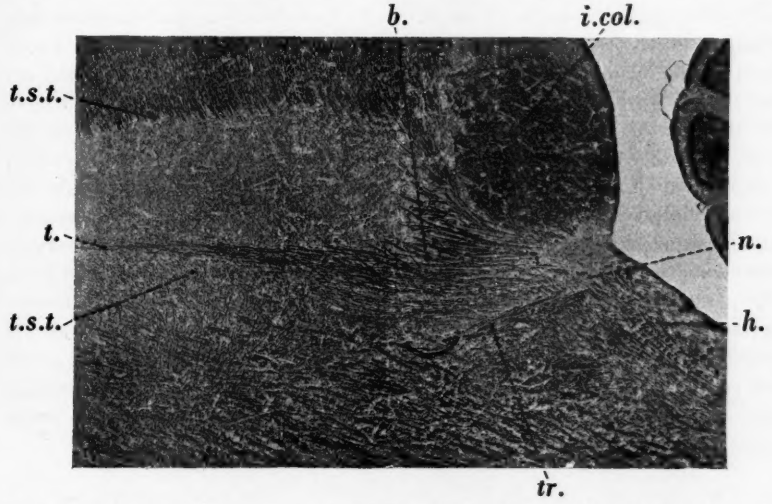

Fig. 4. Microphotograph from a parasagittal section of the mid-brain of cat showing the mesencephalic root of the fifth nerve. *h.* head; *n.* neck; *b.* body; *t.* tail; *tr.* trochlear nerve. × 14.

increases, new fibres are added to it, and more cells appear along its course. At this point the root lies in the lateral part of the central grey substance surrounding the aqueduct on the medial aspect of the concavity of the tecto-spinal tract. Above the level of the caudal border of the tecto-spinal tract, and opposite the posterior colliculus, there is a sudden increase in the size of the root, due to fibres joining it from cells lying either dorsal or ventral to the level of the root bundle. The mesencephalic root reaches its maximum size opposite the anterior medullary velum; from there onwards to the motor nucleus of the fifth nerve the diameter of the root remains more or less constant.

The outline and position of the mesencephalic root in the mid-brain are shown in fig. 4. In the region of the corpora quadrigemina, the root is directed backwards to a point near the entrance of the fourth nerve into the anterior

medullary velum. Below that point, the mesencephalic root is bent ventrally, forming an obtuse angle with its more anterior fibres, and descends medially to the brachium conjunctivum to emerge from the brain with the trigeminal nerve.

The root may therefore be described as consisting of a head, neck, body and tail. The head lies distal to the obtuse angle bend on the course of the root, while the neck occurs at the angle. The tail is the anterior extension in the region of the superior colliculus. The body-like part in between the head and the tail is made up of fibres which are added to the root from an accumulation of cells on a level with the oculomotor nucleus.

The cells of the mesencephalic nucleus are seen to be scattered over a much wider area than that occupied by the root. In a cranio-caudal direction they extend from the region of the posterior commissure to a point about 2 mm. distal to the decussation of the fourth nerve. The main cell mass in the cat does not, as a rule, reach as far caudally as the level of the motor nucleus of the fifth nerve. Occasionally, however, cells may be seen extending to this level. Rostrally the mesencephalic cells near the posterior commissure occupy a more medial position than those caudally situated. Dorso-ventrally the mesencephalic cells border the central grey substance of the aqueduct and are usually situated medial to the tecto-spinal tract. A few of the cells may be located in the reticular formation lateral to the tract; processes from these cells pass through the fibres of the tract to reach and accompany the mesencephalic bundle (fig. 5). An increase and accumulation of the cells of the mesencephalic nucleus occur opposite the third nerve nucleus and also opposite and caudal to the decussation of the fourth nerve. When followed ventrally some of the cells may accompany the tecto-spinal tract as far as the oculomotor nucleus.

The fourth nerve and the relationship it bears to the mesencephalic root

On reaching the level of the mesencephalic root, fibres of the trochlear nerve appear actually to form an interlacing mass with fibres from the mesencephalic root; the fourth nerve rootlets were seen, in more than one series, to lie in the same sagittal plane as the mesencephalic bundle (fig. 4). Mesencephalic cells are to be found on the course of the nerve. The fourth nerve crosses the mesencephalic root just posterior to the inferior colliculus and at the bend on the course of the root. As can be seen in fig. 6, the fourth nerve proceeds caudally and laterally, more or less parallel and slightly dorsal to the further course of the mesencephalic root. The fibres of the nerve soon change their course and bend medially at an acute angle towards the velum. Cells from the mesencephalic nucleus are still seen on this part of the nerve accompanying it as far as the anterior medullary velum. They are now more closely related to the fourth nerve than they are to the mesencephalic root and some of them are sending their processes directly into the velum. Fig. 7 shows quite clearly the grouping of the mesencephalic cells around the nerve,

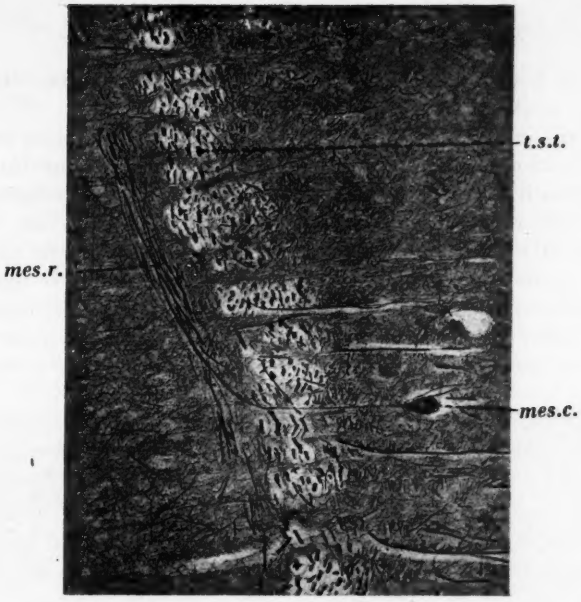

Fig. 5. Microphotograph from a horizontal section through the mesencephalon of cat showing a mesencephalic root cell lateral to the tecto-spinal tract; its process passes through the fibres of the tecto-spinal tract and then joins the mesencephalic root. × 104.

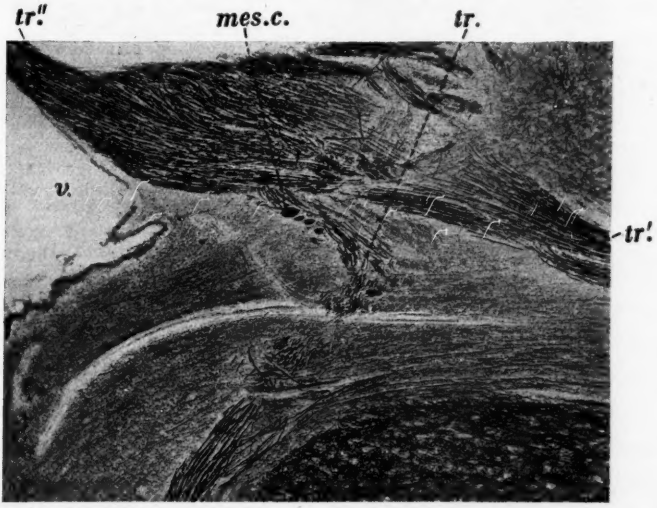

Fig. 6. Microphotograph from a horizontal section through the decussation of the fourth nerve showing the entrance of one of the fourth nerves into, and the exit of the nerve of the opposite side from, the anterior medullary velum. Mesencephalic root cells are to be seen on the course of the nerve entering the velum and one of the cells is directing a process towards it. × 50.

and, further, how the fibres of these cells encircle and penetrate the trunk of the nerve.

In a series in which the mid-brain was cut in a sagittal plane and slightly obliquely, a microphotograph was taken of one of the sections made through the central path of the fourth nerve just before it comes into relation with the mesencephalic root. The same nerve trunk, transversely cut, was again photographed on the opposite side after its decussation in the anterior medullary velum. The number of the constituent fibres of the fourth nerve, inside the brain and at a level ventral to that of the mesencephalic root, was 483. After the nerve has passed through the mesencephalic root and nucleus, and after it has crossed the anterior medullary velum to the opposite

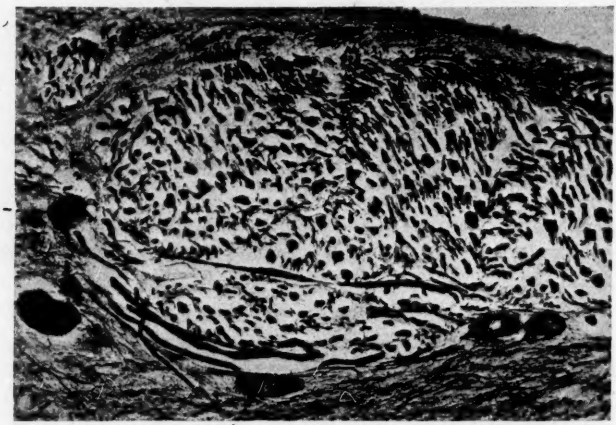

Fig. 7. Microphotograph from parasagittal section of the fourth nerve at the root of the anterior medullary velum showing fibres from the mesencephalic root cells encircling and passing through the trochlear nerve fibres. × 192.

side, the number of its fibres rose to 1075. In another instance, the number of the fibres that constituted the nerve trunk before its passage through the mesencephalic root was 345; after its emergence from the velum, 693. This increase in the number of fibres must be partly, if not mainly, due to the addition to the fourth nerve of extra fibres from the cells of the mesencephalic nucleus.

The tecto-spinal tract in relation to the mesencephalic root

Fibres of the tecto-spinal tract arise within the tectum of the mesencephalon "from cells in the superficial as well as the middle grey stratum" of the superior colliculus (Papez, 1929). According to Ranson (1931), more fibres come from the superior than from the inferior colliculus. The course taken by this tract could be better studied in both horizontal and sagittal sections than in transverse ones. A horizontal section through the dorsal part

of the corpora quadrigemina cuts the fibre tract transversely. The tract appears as a curved line concave inwards and bordering the periventricular grey matter of the aqueduct. Its extent is more or less limited to the region of the anterior colliculus. This linear form that the tract exhibits at dorsal levels broadens gradually as the fibres advance in a ventral direction. The fibres converge as they sweep ventrally towards their decussation and the tract spreads over an area which, though shorter in cranio-caudal diameter, is much broader medio-laterally.

The mesencephalic root keeps a close relationship to the medial aspect of the tecto-spinal tract. The mesencephalic cells are intimately associated with this tract and they accompany it farther cephalad than does the mesencephalic root itself. While the majority of the cells of the mesencephalic nucleus are scattered on the medial side of the tract, many of the cells were seen to lie among the fibres of the tract and even also lateral to it, the processes of which to join the root have to pass through the tract fibres (fig. 5).

Dorsally, the cells can be seen as soon as the tecto-spinal fibres make their appearance. As more fibres come into view more cells appear and they accompany the tract ventrally till near the level of the oculomotor nucleus. These observations raised the question of the possibility whether or not some of the processes from the cells of the mesencephalic nucleus join the tecto-spinal tract. While going through the series special attention was directed to such a connection. Occasionally a mesencephalic cell was seen sending a process towards the tecto-spinal tract. Fig. 8 is a microphotograph of a cell with its process directed towards the tract; the cell lies lateral to the tract and at a more dorsal level than that of the mesencephalic root. The situation of this cell, and the size and direction of its process, suggests that in this case the cell process runs with the tract rather than with the root.

Fig. 9 shows a mesencephalic cell amidst the fibres of the tecto-spinal tract. While the cell is at the same level as the anterior end of the mesencephalic root, its process goes ventrally with the fibres of the tecto-spinal tract. It is quite obvious that this process is foreign to the mesencephalic bundle and that it is carried through the tecto-spinal tract, possibly, to some other pathway.

It was because of the arched course of the tecto-spinal tract that much difficulty was encountered in following a nerve fibre out of its cell for any considerable distance in sections cut at 15 μ thickness. The method of investigation will have to be extended before further connections between the mesencephalic root and the tecto-spinal tract can be discovered.

The tecto-spinal tract at the level of the oculomotor nucleus

Fibres of the tecto-spinal tract are usually heavily medullated, and so are easily recognised by their coarser calibre. Thinner fibres are also noticeable among the coarser ones. While encircling the central grey substance, the tract fibres run in separated groups of from two to eight; sometimes there may be twenty of them in each bundle. Opposite the middle of the oculomotor

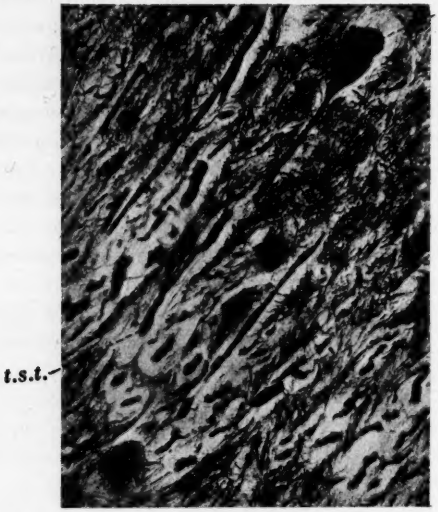

Fig. 8. Microphotograph from an oblique section through the tecto-spinal tract showing the process from a mesencephalic root cell directed towards the tract. ×242.

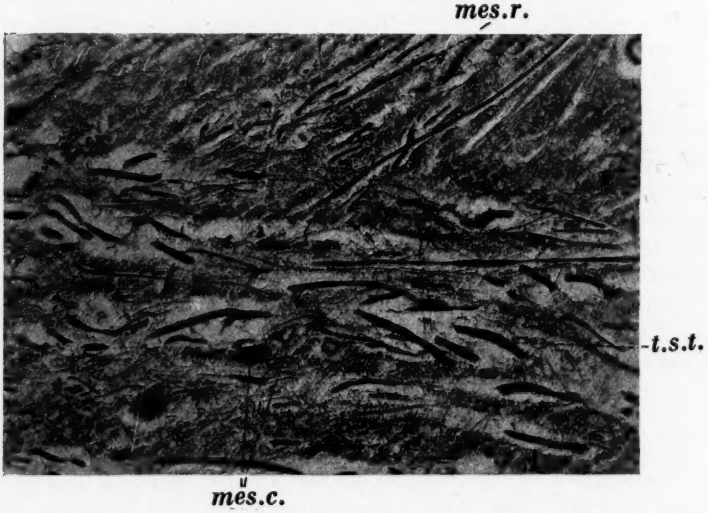

Fig. 9. Microphotograph from a parasagittal section of the mid-brain of cat showing a mesencephalic root cell on a level with the mesencephalic root bundle and sending a process ventrally with the tecto-spinal tract. ×192.

nucleus, the tecto-spinal tract lies at the lateral border of the posterior longitudinal bundle. At that level the tract occupies a more or less quadrangular area and the fibres begin to be directed medially towards their decussation. Dorsally situated fibres pass through the posterior longitudinal bundle and cross the middle line in the dorsal part of Meynert's fountain decussation. Fibres more ventrally placed pass between the rootlets of the third nerve before reaching the middle line.

Fig. 10 is a horizontal section through the fountain decussation of Meynert just ventral to the level of the oculomotor nucleus. The rootlets of the third nerve are seen to be cut transversely. Bordering them posteriorly is the

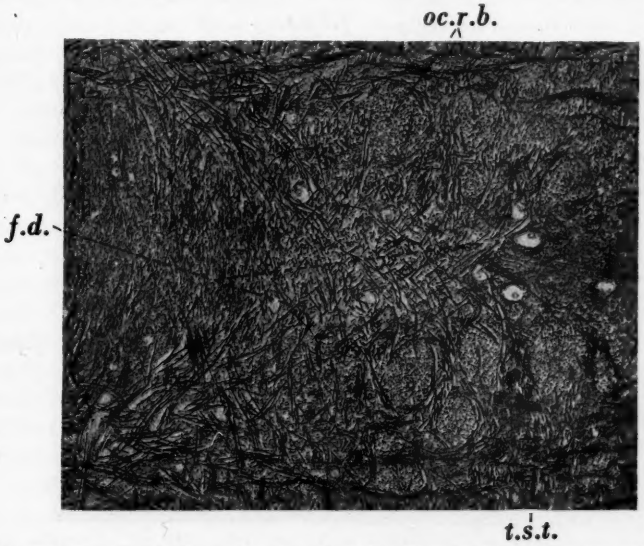

Fig. 10. Microphotograph from a horizontal section through the tegmentum of the mesencephalon at the level of the fountain decussation of Meynert showing the rootlet bundles of the third nerve and fibres of the tecto-spinal tract arching in between. ×316.

fountain decussation of Meynert which lies cephalad to the decussation of the brachia conjunctiva (the latter decussation does not appear in the photograph). Lateral to the rootlets of the third nerve, fibres from the tecto-spinal tract are in view. Caudally situated fibres pass directly medially, while those in a cephalad position run medially and backwards to reach their decussation. In that part of their course the tract fibres run between, and sometimes across, the bundles of the third nerve rootlets. As a rule, fibres that are about to decussate do not penetrate through the third nerve bundles, but wind around their periphery or entwine themselves between these bundles to reach the middle line. On the other hand, a few of the fibres—coarse ones—were found to penetrate the bundles from the third nerve (see fig. 11). These fibres were

at first seen to be obliquely placed, later they appeared to be directed vertically, viz. parallel to the third nerve fibres.

There is a communication, therefore, from the tecto-spinal tract to the root fibres of the oculomotor nerve. Also, cells from the mesencephalic nucleus of the fifth nerve, as is shown above, are contributing fibres to the tract (figs. 8, 9). One would expect the fibres added to the tecto-spinal tract by cells of the mesencephalic root to be the same fibres which again leave the tract and are continued in the oculomotor nerve.

In this investigation no detailed study has yet been made of the tecto-spinal tract after it has crossed to the opposite side. An interesting observation,

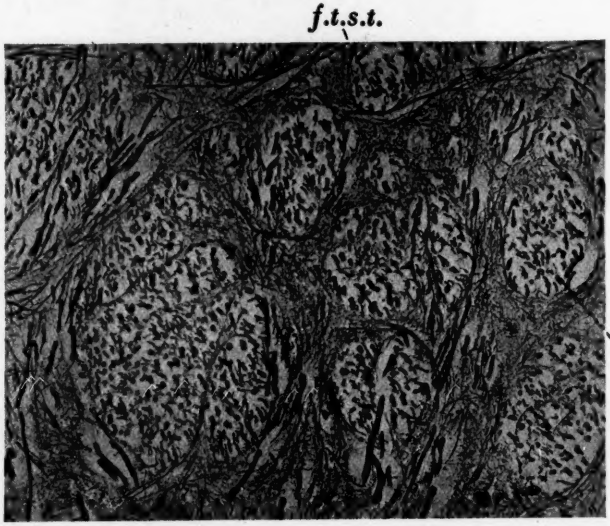

Fig. 11. Microphotograph from a section across the rootlet bundles of the third nerve in the tegmentum of the mid-brain showing fibres from the tecto-spinal tract which have penetrated these bundles, while the rest of the fibres run medially and backwards to their decussation. × 192.

however, was the finding of two nerve cells on the course of the tecto-spinal tract at a considerable distance caudal to Meynert's decussation and also caudal to the crossing of the tract through the brachium conjunctivum. Morphologically, these cells are exactly similar to those of the mesencephalic nucleus; most probably they are mesencephalic cells that have migrated thus far on the course of the tecto-spinal tract.

DISCUSSION

Afferents from the ocular muscles and their possible place of origin

It has been known for some years that afferent fibres reach the ocular muscles; both their muscular and tendinous endings have been figured and described—Huber (1899, 1900) and Tozer and Sherrington (1910)—yet the cells of origin of these fibres and the course they pursue to reach their destination have remained a matter of speculation. The third, fourth and sixth nerves arise from motor efferent nuclei in the brain stem and have always been regarded as motor nerves. Attention was therefore given to the fifth nerve, and the Gasserian ganglion has been thought to be the site of origin of these sensory fibres. It is true that a connection is sometimes seen between the ophthalmic division of the fifth and the third nerve (cf. Stibbe, 1929, 1930), but no one has yet traced the individual fibres of such a connection to endings on an eye muscle fibre.

Sherrington (1897, 1898) and later Tozer and Sherrington (1910) have shown that division of the ophthalmic branch of the fifth nerve leaves unaffected the sensory fibres seen in large numbers at the musculo-tendinous junction of an eye muscle. On the other hand these sensory fibres degenerate on section of the third, fourth or sixth nerves. Sherrington stated that these fibres are neither contained in the optic nerve nor in the ophthalmic branch of the fifth nerve, but pass within the trunks of the ocular nerves themselves. Attention was then directed to various localities, other than the Gasserian ganglion, from which these sensory fibres might be derived. Three regions in particular were considered: (i) the motor nuclei of the ocular nerves themselves, (ii) the ganglion cells that are sometimes seen on the ocular nerves, and (iii) the mesencephalic nucleus of the fifth nerve.

(i) Reference has already been made to the work of McLean (1926) and his suggestion that the smaller cells in the motor nuclei of the ocular nerves may give rise to the proprioceptive fibres of the ocular muscles. In this particular regard, it seems to me that Woollard (1931) correctly refutes such a possibility when he writes: "It would be unexpected and against all principles in the architectonics of the central nervous system to expect to find the sensory cells of the eye muscles intermingled with the motor nuclei."

(ii) As to the ganglion cells that are met with on the trunks of the ocular nerves, they neither exist constantly nor does their number suffice to supply all the proprioceptive fibres of the eye muscles. Nicholson (1924), in a full term human foetus, counted thirty cells on the root of the third nerve; the most proximal cells were at 2·8 mm. from the superficial origin of the nerve, and the most distal ones at about 4·0 mm. out on the fibres. Within the orbit three ganglia were found on the branch from the third nerve to the inferior oblique muscle and one ganglion on the branch to the internal rectus. The number of the cells in these ganglia was fourteen, and a total of only forty-our was therefore found on the entire length of the third nerve and its intra-

orbital branches. No ganglion cells were found on the trunk of the fourth nerve, while on the sixth nerve one ganglion containing approximately thirty cells was found. Nicholson wrote: "Investigation was not made upon the intracranial roots of the sixth and fourth nerves, as they were lost in the removal of the brain."

Though in all probability these cells are sensory in character and their processes approach the ocular muscles, it is quite obvious that the forty-four cells seen by Nicholson on the course of the third nerve, the presence of which, as we know, is rather inconstant, cannot possibly be the source of all, or even of the greater portion of the afferent fibres of the muscles supplied by the third nerve. Also the close relationship of these ganglion cells to the ocular muscles minimises the opportunity for the bifurcation of their fibres. On the other hand, if these ganglion cells were sensory units that have migrated from some other parent sensory nucleus, it would be only natural to include the mesencephalic nucleus of the fifth nerve among places from which these cells could have been derived. These ganglion cells have been seen on the intracranial part of the third nerve above the level where connections from the ophthalmic branch of the fifth may enter this nerve. Nicholson and others could find none of these cells on the fourth nerve; Nicholson, however, did not examine the intracranial root of the fourth nerve. Quite probably, it is because of the relatively great length of the fourth nerve that these cells were rarely seen on its distal path, and it is likely that these cells might have been found with the same frequency with which they are seen on the third and sixth nerves, if the fourth had been examined at its exit from the dorsum of the mesencephalon.

(iii) In addition to the above-mentioned views on the subject, the mesencephalic nucleus of the fifth nerve has been held as a possible place of origin of the sensory fibres of the ocular muscles.

The mesencephalic nucleus of the fifth as a proprioceptive organ for the extra-ocular muscles

That the mesencephalic root is sensory in function and that it supplies the proprioceptive fibres for the muscles of mastication is now accepted by most authors—Willems (1911), Kosaka (1912), Allen (1919), Freeman (1927), Weinberg (1928). While some of the workers have supported the view of a relationship of this root to the extrinsic ocular muscles, others have not admitted it, but the ground for this denial has been the failure to demonstrate the connection rather than the production of positive evidence to the contrary.

In their experiments on cats and monkeys, May and Horsley (1910) reported that no degeneration occurred in the ocular nerves after intracerebral section of the mesencephalic root; it was therefore concluded that the mesencephalic root is not connected with the innervation of the eye muscles. For many reasons this conclusion seems unjustifiable. It is quite possible to

secure division of the mesencephalic root itself without much injury to those cells of the mesencephalic nucleus associated with the ocular muscles. For these cells and their processes may escape injury through being situated distant from the point of division of the root. It is also difficult to regard as decisive the teasing method which May and Horsley used in their search for degenerated fibres. When one further reads that they were unable to demonstrate, after mesencephalic root section, any degeneration in the branches of the fifth nerve distal to the Gasserian ganglion, a considerable doubt arises as regards their conclusion on the innervation of the ocular muscles.

In 1912 Tozer was unable to demonstrate any chromatolysis in the cells of the mesencephalic root after section of the third or fourth nerves. The idea that some of these large globular cells might prove to be the source of these afferents—she said—"must I think be given up." Tozer gave no description of her method of study or of the time she allowed for chromatolysis to occur. The chromatolytic reaction in the cells of the mesencephalic root seems to differ from that in multipolar or other sensory cells. Willems (1911) referred to the irregularity with which the mesencephalic cells react to degeneration and assumed that, in one of his experiments, these vesicular cells, after having presented a deep reaction, must have again approached a semi-normal condition. We also know that localisation of the cells of the mesencephalic nucleus associated with the ocular muscles has not yet been made; it is not unlikely that they are scattered widely among those in connection with the muscles of mastication. Obviously it is not easy to locate, in a transverse section of the mid-brain where only a few of the mesencephalic cells are seen, those cells that would have degenerated after severance of an ocular nerve.

Contrary to Tozer's results, Freeman (1925, 1927), after removal of the whole of the orbital contents in the cat, was able to demonstrate on the operated side chromatolysis and shrinkage of the mesencephalic root cells at the level of the oculomotor nucleus and rostrally; on the opposite side degeneration took place in cells lying at the level of the trochlear nucleus. In an animal (cat) in which only the eye-ball was enucleated, the mesencephalic root and cells on both sides were found healthy. Woollard (1931), after section of the third nerve in the rabbit, also reported chromatolysis in the cells of the mesencephalic root. Added to the findings of Freeman and Woollard is the fact that division of the mandibular branch of the fifth nerve does not lead to degeneration of the whole of the cells of the mesencephalic root. The experiments of Willems, contrary to his expectation, showed that only a little more than half the cells of the mesencephalic root (51 per cent.) degenerate on avulsion of the muscular branches of the mandibular nerve. From this, one is justified in inferring that the mesencephalic root cells which persist in a sound condition after section of the mandibular division of the fifth nerve, are those cells from which the afferents of the ocular muscles are derived.

The results of my experiments have confirmed those performed by Tozer and Sherrington (1910). Section of the third nerve results in degeneration of

all the motor and sensory fibres contained in the muscles supplied by this nerve, except for a few minute fibres which are not in themselves sufficient to furnish the afferent system of these muscles. The proprioceptives of these muscles must therefore leave the brain in the trunk of the third nerve. The mesencephalic root of the fifth nerve is the place in the mid-brain which one would expect to be the source of these sensory fibres. The anterior part of the nucleus of the mesencephalic root is in close relationship with the tecto-spinal tract, and some of the mesencephalic cells lie among the fibres of the tract and can be seen to extend as far dorsally as do the tract fibres. Ventrally, they may accompany the tract as far as the oculomotor nucleus. Two of the cells have been found contributing fibres to the tract, which in turn gives a connection to the third nerve rootlets. It is therefore justifiable to conclude that the proprioceptive fibres from the muscles supplied by the third nerve take origin from those cells of the mesencephalic nucleus which are related to the tecto-spinal tract. The fibres accompany the tract as far as the level of the oculomotor nucleus, where, as the tract bends medially to decussate, the fibres from the cells of the mesencephalic nucleus of the fifth run into rootlets of the third nerve.

In the case of the fourth nerve, cells from the mesencephalic nucleus have been found accompanying this nerve towards the anterior medullary velum and contributing fibres to it (see figs. 6 and 7). This connection between the trochlear and the vesicular cells of the mesencephalic root has been previously emphasised by Golgi, though no reference was made by him to their being the sensory component of this nerve. His actual words read as follows: "Dans ces rapports, comme il est facile de constater que le prolongement de ces cellules isolées s'unit aux fibres formant la valvule de Vieussens, il serait difficile d'obtenir une autre preuve plus positive de la participation directe des cellules monopolaires à la formation du pathétique." In one experiment, in which the fourth nerve was cut, my results again were in complete agreement with those obtained by Tozer and Sherrington, viz. degeneration, save for very few fine fibres, of all the motor and sensory fibres in the superior oblique muscle. The number of the fibres constituting the trunk of the fourth nerve was counted, first in the central path of the nerve below the level of the mesencephalic root, and then after the nerve emerges from the anterior medullary velum. The number of nerve fibres was a little more than doubled after the decussation of the nerve. This large increase in number cannot be solely due to the bifurcation of the fibres, but must be partly or mainly due to the addition of new fibres to the fourth nerve; these new fibres can only have come to it from the cells of the mesencephalic root.

Having shown that the number of the fourth nerve fibres increases enormously after passing through the area of the mesencephalic root and nucleus, that section of the fourth nerve degenerates all the motor and sensory endings in the superior oblique muscle, and that some of the vesicular cells of the mesencephalic nucleus accompany the fourth nerve and send their

processes with it into the anterior medullary velum, the author believes that he has produced the strongest evidence that the proprioceptive fibres of the superior oblique muscle arise in the cells of the mesencephalic nucleus of the fifth nerve and leave the brain in the trunk of the fourth.

No special study has yet been made of the sixth nerve. The finding of two of the mesencephalic cells on the course of the tecto-spinal tract caudal to the fountain decussation of Meynert suggests the possibility that the afferent fibres of the external rectus, as in the case of the muscles supplied by the third nerve, may arise from the cells of the mesencephalic nucleus of the fifth nerve and accompany the tecto-spinal tract as far as the level of the abducens nucleus, where they may then leave the tract to join the rootlets of the sixth nerve.

The source of the minute fibres which remain healthy in an ocular muscle after severance of its nerve

After combined section of the three ocular nerves and of the ophthalmic division of the fifth nerve, Tozer and Sherrington (1910) found that a few sparse minute fibres persist undegenerated in the extra-ocular muscles. In the case of the third nerve there were from six to twelve of these fibres for each muscle and their number for any one of the muscles never exceeded twenty-five. These fibres, the authors state, appeared to be derived from the ciliary ganglion: "the fibres resemble in size and appearance those of the short ciliary nerves proceeding from the ciliary ganglion" (p. 453). In the course of the experimental part of this investigation, these fine fibres have been observed to persist after degeneration of all other fibres. Their number, however, it is believed, in some of the muscles may slightly exceed the numbers reported by Tozer and Sherrington. On examination of material obtained from a cat sacrificed 27 days after section of the oculomotor nerve, minute fibres similar to those which persist healthy in the ocular muscles were clearly observed to arise from cells of the ciliary ganglion and run through the degenerated trunk of the third nerve (see fig. 3). It is through the trunk and branches of the third nerve that these fibres may ultimately reach the ocular muscles, probably to terminate in the walls of blood vessels. This communication from the ciliary ganglion to the third nerve confirms Sherrington's view.

It seems reasonable to assume that some of these fine fibres are derived from the unipolar ganglion cells occasionally seen on the third or sixth nerve. These cells could be demonstrated, not only in the intracranial course of the nerves, but also intra-orbitally as far as the actual entrance of the nerve into muscle.

Another possible source of some of these fibres is the Gasserian ganglion. It is not unlikely that some of these fine fibres, probably along with an insignificant number of coarser ones, come from this ganglion. This may explain the connection anatomically described as existing between the ophthalmic division of the fifth and the third nerve, and also partly explains the occasional occurrence of degeneration of a few nerve fibres in some of the ocular muscles following section of the ophthalmic branch of the fifth nerve

or injury of the Gasserian ganglion. But this degeneration has been regarded as mainly due to injury of the ocular nerves at the time of operation.

SUMMARY AND CONCLUSIONS

1. Section of the third and fourth nerves at exit from the brain results in degeneration of all the motor and sensory fibres and endings in the muscles supplied by these nerves, except for a few minute fibres which arise from cells distal to the cut and which are not sufficiently numerous to constitute the proprioceptive system of these muscles. These nerves are therefore sensori-motor and the greater portion of the afferent supply of the ocular muscles they supply is already incorporated in the nerve trunks as they leave the brain.

2. The fourth nerve conveys from cells of the mesencephalic nucleus of the fifth nerve the proprioceptive fibres of the superior oblique muscles, as is shown by the mesencephalic root cells implanted on the course and entrance of the fourth nerve into the anterior medullary velum, and also by the marked increase in the number of its fibres after having crossed the mesencephalic root.

3. The cells of the mesencephalic nucleus of the fifth nerve, in the region of the superior colliculus, are intimately related to the tecto-spinal tract. They are seen medial to, amidst and sometimes lateral to the tract fibres. Fibres from these cells appear to run ventrally with the tecto-spinal tract towards the oculomotor nerve.

4. There is a communication from the mass of fibres of the tecto-spinal tract to the bundles of rootlets of the oculomotor nerve.

5. It is suggested that the mesencephalic root cells, in relationship with the tecto-spinal tract, send out sensory fibres which accompany the tract towards the oculomotor nucleus, at which point they run with the third nerve to the ocular muscles.

6. A communication from the ciliary ganglion to the oculomotor nerve has been demonstrated.

This investigation is being carried further to trace the course of the sensory fibres of the sixth nerve and to obtain further evidence concerning those of the third nerve.

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ABBREVIATIONS

s.n.f.	Sensory nerve fibres.
mes.c.	Mesencephalic root cells.
mes.r.	Mesencephalic root.
t.s.t.	Tecto-spinal tract.
v.	Fourth ventricle.
i.col.	Inferior colliculus.
tr.	Fourth nerve entering the velum.
tr.'	Fourth nerve emerging from the velum.
tr.''	Decussation of fourth nerve.
cil.g.	Ciliary ganglion.
deg.oc.	Degenerated third nerve.
c.proc.	Ciliary ganglion cell with a process running into third nerve.
f.d.	Fountain decussation of Meynert.
oc.r.b.	Rootlet bundles of third nerve.
f.t.s.t.	Fibres from tecto-spinal tract entering the third nerve.

THE DEVELOPMENT OF A MEDIAL MOTOR NUCLEUS AND AN ACCESSORY ABDUCENS NUCLEUS IN THE PIG

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The motor nuclei of the cerebral nerves do not conform to the conventional scheme when studied in early embryos which have been treated by silver impregnation methods. Bok (1) and Tello (2) found the cerebral motor nerves of the chick all arising from a medial motor column or nucleus which is superimposed upon the medial longitudinal fasciculus. Windle (3, 4) described the same nucleus in early cat embryos.

There is a similar structure in the pig. In the 11 mm. embryo all motor fibres destined for the trigeminal, facial, glosso-pharyngeal, vagus and accessory nerves arise from a medial motor nucleus that lies deeply embedded in the ependymal zone, dorsal to the medial longitudinal fasciculus (Plate I, figs. 1, 2, 3, 4). The nucleus extends without interruption from the trigeminal nerve well down into the cervical cord. There it fades out beneath the usual somatic motor column. It is largest at the facial level. While most fibres from it enter nerves on the same side, a few cross the mid-line, especially at the level of the facial nerve. The medial motor nucleus impregnates easily with silver, and is conspicuous in otherwise poor preparations.

The abducens and hypoglossal nerves arise in part from the same medial motor nucleus (Plate I, figs. 3 and 4) and in part from the lighter stained ependymal zone just lateral to it. Whether the cells of origin all belong to the medial nucleus is a matter of definition; the chief point is that the two nerves arise somewhat lateral to the others of the hind-brain.

The trochlear and oculomotor nerves arise from similar darkly stained groups of cells. These may be fragments of the medial motor nucleus, but are placed slightly lateral in line with the abducens and hypoglossal nerves.

In embryos of between 11 and 16 mm. most cells migrate outwards from the medial motor nucleus. One group follows the trigeminal nerve and settles down as the chief motor nucleus for that nerve. The great migration occurs between the facial and glosso-pharyngeal nerves (Plate I, fig. 5). The cells collect in the ventro-lateral part of the medulla to form the very large facial nucleus and the scattered nucleus ambiguus.

The site of the medial motor nucleus is not abandoned. It continues to be occupied by a slender strand of fibres mingled with a residuum of cells extending from the trigeminal nerve to the upper levels of the hypoglossal nucleus

(Plate II, figs. 7, 8, 9). The fibres arise for the most part from the included cells; new ones are added, however, from cells that have begun to proliferate in the area of the chief visceral motor nucleus of the adult (Plate II, fig. 9). The whole region now constitutes a primary viscero-motor nucleus that provides fibres for the trigeminal, nervus intermedius, glosso-pharyngeal, vagus and accessory nerves. Plate I, fig. 5, and Plate II, figs. 7, 9, show the viscero-motor fibres leaving the glosso-pharyngeal, trigeminal, and vagus nerves, respectively.

The medial motor nucleus in this modified form is conspicuous in all pig embryos up to 60 mm. It gradually disappears as the permanent visceral motor nuclei develop. It is still traceable in 170 mm. embryos and may persist for a short distance below the genu of the facial nucleus in the adult (Plate II, fig. 10).

At the time of the migration of the facial nucleus a similar phenomenon takes place in the abducens nucleus. In the 16 mm. embryo many abducens fibres fan out laterally (Plate I, fig. 6). Embryos stained with Mallory's phosphotungstic haematoxylin show cell activity in the ependymal zone just above, indicating that the most lateral cells of the original abducens nucleus are moving ventro-laterally (compare Plate I, figs. 3, 6).

In embryos of from 20 to 30 mm. the migrating cells collect as a ventral accessory abducens nucleus (Plate II, fig. 8). The accessory abducens nucleus lies upon the lateral fillet and rubro-spinal tract, in the plane of the superior olive, just cranial to the facial nucleus. The accessory abducens nucleus has a characteristic reticulated appearance. Fibres (or dendrites?) pass superficially into the fillet area. Wavy bundles of axones run dorso-medially to the abducens nerve. Most of these axones turn down into the nerve rootlets. A few turn up towards the main nucleus, and others still pass by the abducens nucleus towards the mid-line. The last may correspond to the scattered medial rootlets of the abducens of the other side.

The accessory abducens nucleus and its fibres are conspicuous landmarks in all pig embryos up to 100 mm. when prepared by the Cajal silver methods. The nucleus can be identified at birth in both Cajal and Weigert preparations. The axones are traced with greater difficulty as the medulla becomes more densely populated. In the adult a distinct nucleus preserves the characters of the embryonic abducens nucleus (Plate II, fig. 10). It should not be confused with the facial nucleus. The true facial nucleus is cut in sections just caudal to the accessory abducens nucleus illustrated, and is as superficial as the superior olive in Plate II, fig. 10. The cells of the abducens nucleus are slightly smaller than those of the facial.

The accessory abducens nucleus has held an obscure place in neurological literature since its discovery in the fowl in 1893. The two most comprehensive studies upon it are by Van Gehuchten (5) and Terni (6). The nucleus is absent in fishes, doubtful in Amphibia and well-developed in Reptiles (Terni). It occurs in birds and rabbits (Van Gehuchten), in the rat (Terni), but not in the mouse

(Cajal(7)). Ziehen(8) considers it doubtful in Man. Mingazzini(9) cites Pacetti as relegating the nucleus to an atavistic status in Man.

Terni regards the accessory abducens nucleus as the innervation of the third eyelid apparatus in Reptiles and Birds. He places the nucleus in proximity to the nucleus of the spinal trigeminal tract, and regards it as the efferent limb of a defence reflex arc which is initiated by stimuli from the skin through the trigeminal nerve. In Mammals the nucleus is associated with the retractor bulbi muscle, which is especially developed in Ungulates. The reported absence of the accessory nucleus in Man would harmonise with this conception, for the muscle is rare in man (Whitnall(10)).

While there is nothing in the pig to contradict such conceptions of the significance of the accessory abducens nucleus, it should be noted that the nucleus is rather intimately connected with the lateral fillet, and would seem therefore a part of the co-ordinating mechanism between the auditory tract and the medial longitudinal fasciculus. The superior olive of the pig has the usual peduncle, which ends obscurely.

The accessory abducens nucleus falls into the group of special visceral motor nuclei in Herrick's scheme of nerve components, and adds one more complication. The nucleus offers another example of neurobiotaxis. It deserves more attention by those investigating the auditory mechanism in lower forms. It might be looked for in human embryos successfully treated with silver impregnation methods.

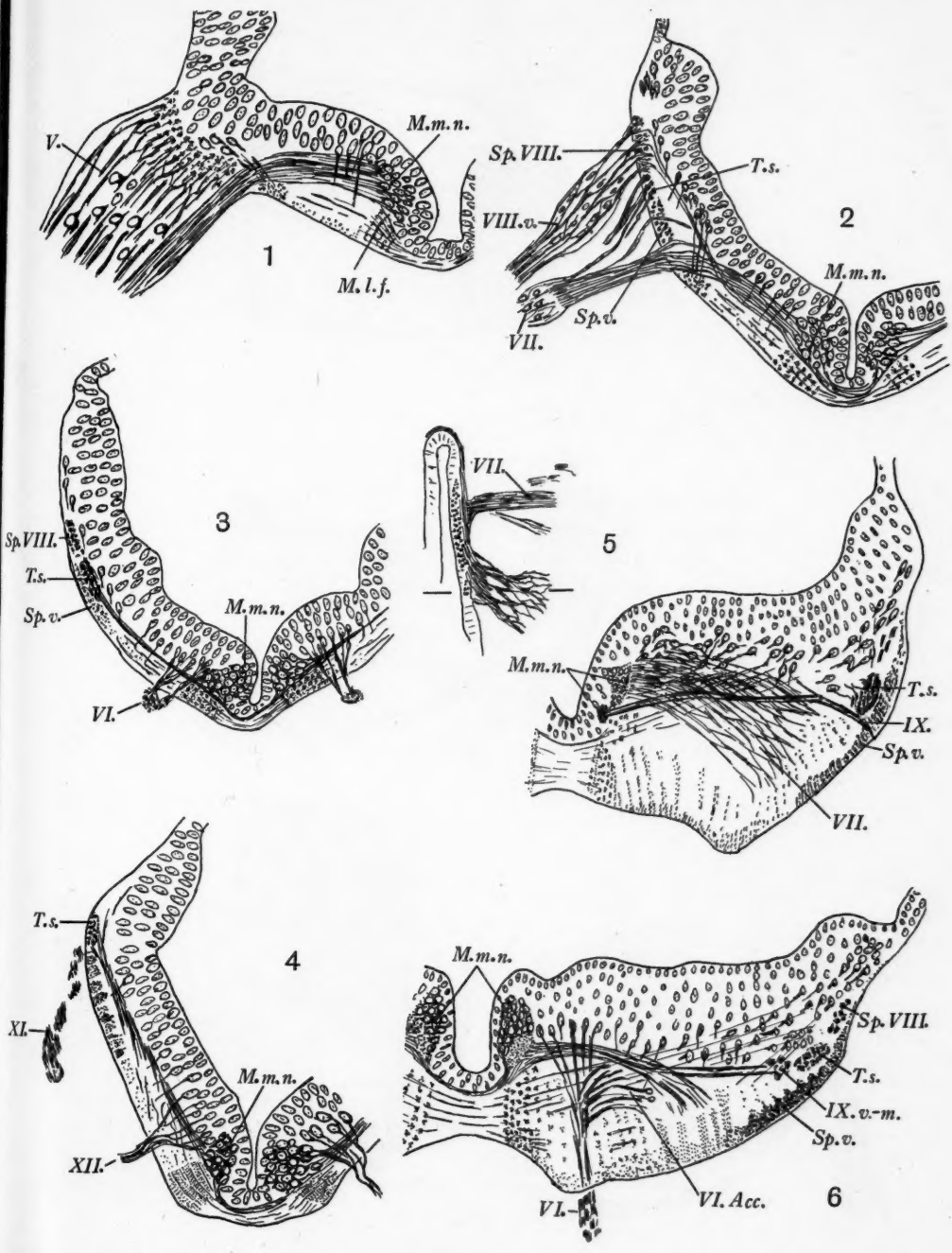
SUMMARY

1. The motor cerebral nerves of the hind-brain of the early pig embryo arise from a medial motor nucleus buried in the ependymal zone over the medial longitudinal fasciculus. The abducens and hypoglossal nerves arise partly from the nucleus and partly from the adjacent ependyma. The oculomotor and trochlear nerves arise from isolated fragments of the same nucleus placed in line with the abducens and hypoglossal centres.

2. After the migration of the facial and chief motor trigeminal nuclei the rest of the medial motor nucleus persists as the primary source of visceromotor fibres for the trigeminal, facial, glosso-pharnygeal, vagus and accessory nerves. The nucleus diminishes with the advent of the adult visceral motor nuclei. Remnants may appear in the adult.

3. At the time of the migration of the facial nucleus a lesser migration of abducens cells occurs. The cells establish an accessory abducens nucleus just rostral to the facial, in the plane of the superior olive and close to the lateral fillet. The nucleus can be found in the adult brain.

I am indebted to Mr A. G. Fairall for the preparation of material used in this study, and to Dr D. G. Revell, who has kindly read the manuscript. I wish to record my thanks to the Banting Research Foundation for a grant for the purchase of materials used in this work.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3
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XI.
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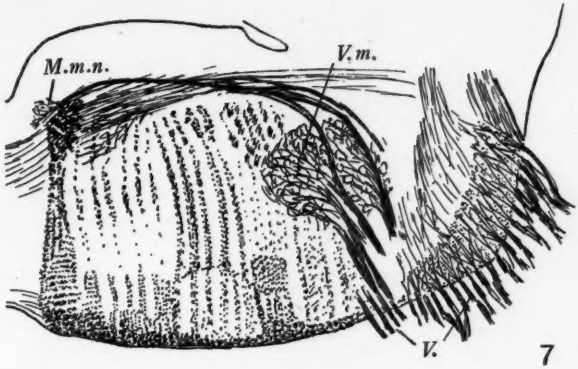

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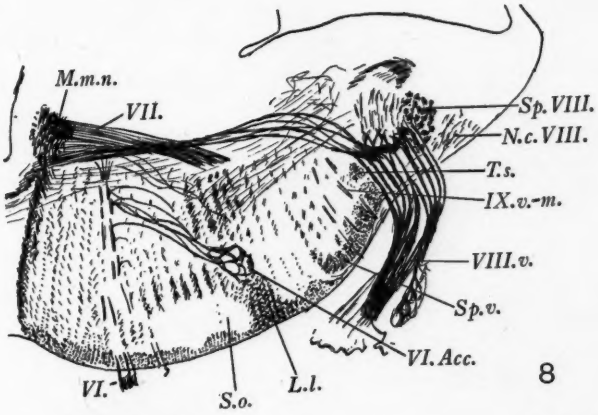

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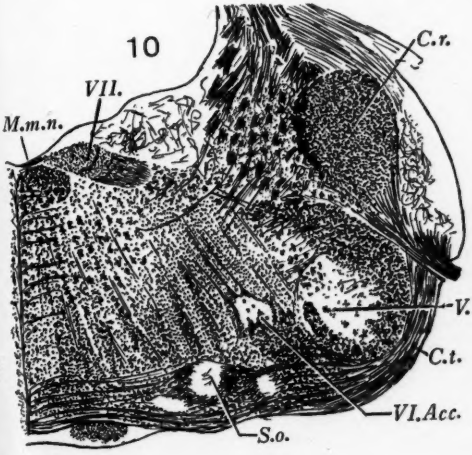

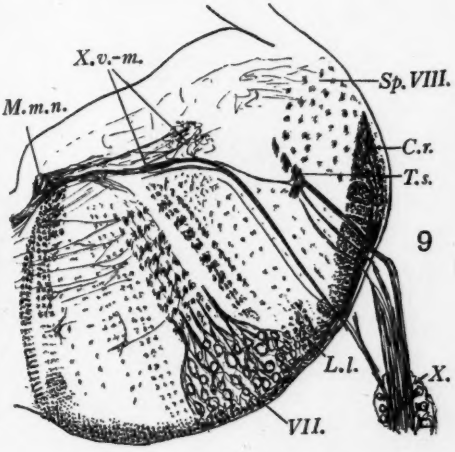

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EXPLANATION OF PLATES

Plate I

Figs. 1–4. Sections from an 11 mm. pig embryo brain, prepared by Ranson's pyridine-silver method. ×66.

Figs. 5, 6. Sections from a 16 mm. pig embryo brain, prepared by Ranson's pyridine-silver method. ×66.

Plate II

Figs. 7–9. Sections from a 28 mm. pig embryo brain prepared by a modification of the Campbell method (Shaner(11)). ×55.

Fig. 10. Section from an adult hog brain. Weigert method. ×6.

ABBREVIATIONS

C.r.	Restiform body.
C.t.	Trapezoid body.
L.l.	Lateral lemniscus.
M.l.f.	Medial longitudinal fasciculus.
M.m.n.	Medial motor nucleus.
N.c.VIII.	Cochlear nucleus.
S.o.	Superior olive.
Sp.v.	Spinal tract of trigeminal nerve.
Sp.VIII.	Spinal tract of vestibular nerve.
T.s.	Tractus solitarius.
V.–XII.	Cerebral nerves.
V.m.	Motor nucleus of trigeminal nerve.
VI.Acc.	Accessory nucleus of abducens nerve.
VIII.v.	Vestibular nerve.
IX.v.-m.	Viscero-motor nucleus and fibres of glosso-pharyngeal nerve.
X.v.-m.	Viscero-motor nucleus and fibres of vagus nerve.

GANGLIA OF THE INTERNAL CAROTID PLEXUS

By Dr A. GELLÉRT

Anatomy Department of the University of Szeged, Hungary

While investigating the relation between the sympathetic system and the cranial nerves, I found in two cross-sections of the internal carotid plexus groups of ganglion cells close to the abducent nerve. In a previous paper (Gellért, 1932) I drew attention to the fact that a group of unmyelinated fibres are to be found adjacent to the ganglion cells, and consequently the ganglia probably belong to the internal carotid plexus. I have since extended my investigations and studied their exact topographical relations and positions, and made a closer examination of the cytological characteristics of the ganglion cells. The material investigated consisted of the internal carotid plexus of both sides from two adults and a child of ten months. I traced the plexus from its origin (the superior cervical ganglion) to that part which is enclosed within the cavernous sinus. Serial microscopical examination was made of the material, which included the internal carotid artery and its immediate surroundings. The prolonged osmic acid method of Kiss (1932) and the Bacsich (1932) method of imbedding, which involves a double imbedding without the use of absolute alcohol, were used to show the different nerve fibres and ganglion cells.

In the bibliography bearing upon the subject I found the following references:

K. Krause, in his handbook (Hungarian translation by Mihalkovics 1882), makes the following statement with reference to the internal carotid plexus: "These branches divide into smaller branches which combine to form a fine, close meshwork about the internal carotid artery. They are seen in great abundance in the lower part of the cavernous sinus and some of them unite to form a small ganglion from which new branches arise. The ganglion of the internal carotid (ggl. caroticas cavernosa) is flat or stellate in shape. It usually lies in the lower region of the cavernous sinus below the abducent nerve at the beginning of the second curvature of the artery or on the anterior or lateral boundary of the internal carotid. Sometimes it is entirely absent and in such cases is replaced by a small and extremely fine plexus at the end of the second curvature...."

Hovelacque (1927) makes the following statement: "Previous writers have described a certain number of ganglia in the plexus, ganglia of Schmiedel, Laumonier and Lobstein in the carotid plexus, ganglia of Krause in the cavernous plexus. Arnold and Cruveilhier deny the existence of the ganglia described in the cavernous plexus. Arnold himself says that the writers were not in agreement as to their position, and that the existence of the ganglia of Krause ought not to be maintained."

In Tandler's (1930) text-book the following may be found: "Ganglionic groups in the form of small flat bodies are frequently found in this plexus."

I could find no further references to these ganglia in spite of a careful and thorough search. It is interesting to note that recent text-books which discuss the sympathetic system make no mention of the fact that ganglia are to be found in the internal carotid plexus. The text-books to which I particularly refer are the following: Müller (1924), Schilf (1926), Delmas and Laux (1933). This omission is probably to be explained by the authors being influenced by the definite denial of the existence of these ganglia made by Cruveilhier and Arnold. Recent investigators have not taken the question into consideration, and the ganglion as described by Krause has apparently been forgotten.

The results of my investigations are as follows. The same relations exist in the internal carotid plexus of either side with the exception, in one instance, of one or two cells. No ganglion cells were found in the region extending from the superior cervical ganglion to the beginning of the cavernous sinus. The plexus here was composed entirely of unmyelinated fibres. Within the cavernous sinus and in close proximity to the abducent and ophthalmic nerves I found small ganglia, usually intermingled with the unmyelinated fibres of the plexus.

The description of the topographical relationships of the ganglia is based on those found on the left side in the ten months old child. The first group of ganglion cells in the plexus was found in a rather large bundle of unmyelinated fibres. The ganglion was about 0·3 mm. in length and in its widest part 10–11 ganglion cells were found. Passing cranially towards the cavernous sinus a few ganglion cells were found to occur sporadically between the bundles of unmyelinated fibres. At the same level the bundle of unmyelinated fibres, within which the first ganglion was found, contained another group of ganglion cells, 0·5 mm. long, in which 7–8 cells were to be seen in each section. Further cranialwards was a region about 3 mm. in length, which was entirely free of ganglion cells. This was succeeded by a ganglion 0·1 mm. long and containing 8–9 cells per section, situated on the outer side of the abducent nerve and close to the ophthalmic nerve. This ganglion was continuous for about 5 mm. with a few cells scattered among the bundles of unmyelinated fibres. Further forwards a relatively large ganglion consisting of 17–18 cells appeared on the inner side of the abducent nerve between it and the internal carotid artery. With it two smaller ganglia in proximity to the ophthalmic nerve were also seen (fig. 1). In this region, at intervals of 0·1–0·2 mm., sections with none alternate with those showing ganglion cells. Here also two other ganglia were found, one of which is 0·5 mm. in length. Beyond this region an additional chain of these ganglia was situated between the ophthalmic and abducent nerves, but nearer to the former. This chain was about 1·1 mm. in length. A ganglion was also to be seen on the inner side of the abducent nerve, probably a member of the aforementioned chain. On the lateral surface of the ophthalmic nerve another ganglion 0·4 mm. in length was present. Thirty to forty ganglion cells were found in each section of the larger of these ganglia (see

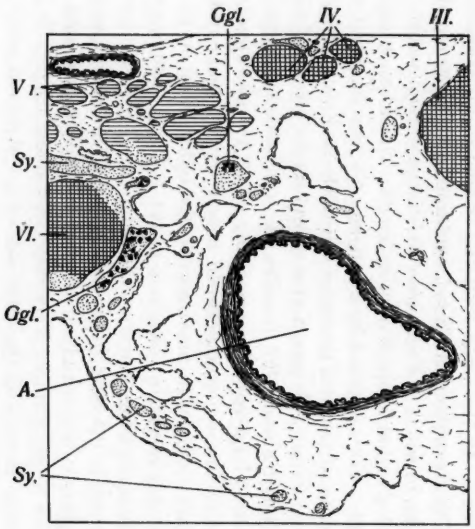

Fig. 1. Ganglion cell group on the inner side of the abducent nerve.

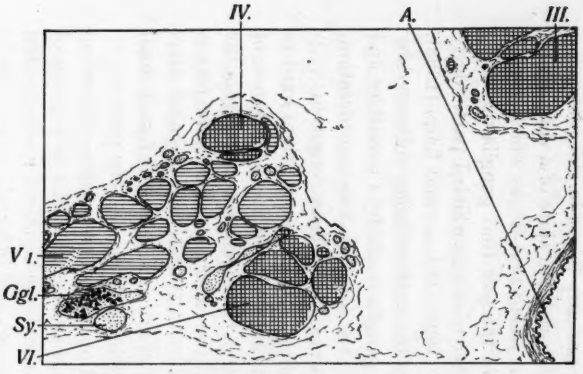

Fig. 2. Group of ganglion cells between VI and V.

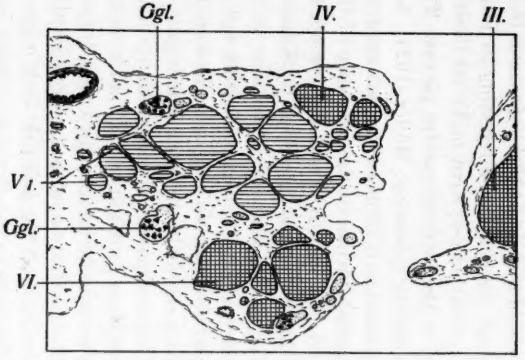

Fig. 3. Group of ganglion cells within the cavernous sinus located on the inner and outer side of VI and one group on the outer side of V about 0·5 mm. from fig. 2.

fig. 2). Continuous with this area of the section there followed an area about 0·5 mm. wide, which was free from ganglion cells. Then a ganglion 0·1 mm. in length was found in the front end of the cavernous sinus, situated some distance from the abducent nerve among the unmyelinated bundles of the internal carotid plexus (fig. 3).

From the foregoing it can be realised that within the cavernous sinus, and in close proximity to the abducent nerve there are two gangliated chains, one on the medial side of the nerve, between it and the internal carotid artery, the other in proximity to the ophthalmic nerve. The ganglia are closely associated with the bundles of unmyelinated nerves of the internal carotid plexus either within them, between them, or close to them.

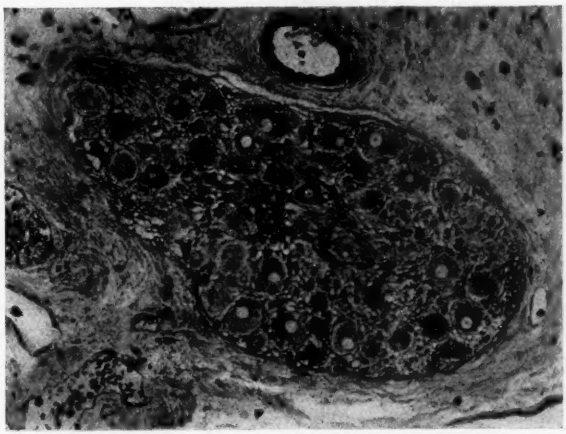

Fig. 4. Ganglion in the internal carotid plexus.

The ganglion cells found in these ganglia when treated by the prolonged osmic acid method of Kiss show a remarkable likeness to those found in other cranial ganglia (fig. 4). Some of the ganglion cells are large and round, with a pale cell body, others are small, multipolar, with the protoplasm darkly stained. These two different types of cells are found together in each ganglion, but in certain areas of the ganglion the dark cells predominate, while in others the paler are more numerous. In consideration of the fact that these ganglia are in close connection with unmyelinated fibres, I am of the opinion that the ganglia may be sympathetic.

Separation of the fibres which have their origin in the ganglia from those of the unmyelinated bundles of the plexus is quite impossible owing to the close connection between them. This strengthens my belief that a large number of these fibres, including the unmyelinated of the carotid plexus, pass into the ophthalmic nerve. Should similar ganglia be found in higher Mammals (I am

at the present time making such investigations) it will be a simple matter to understand why certain investigators, e.g. Windle (1926), after having removed the superior cervical ganglion still found unmyelinated fibres in the ophthalmic nerve. Further, although unmyelinated fibres from the small dark cells in the Gasserian ganglion (Kiss, 1932) enter the ophthalmic nerve, I do not accept the view that sensory unmyelinated fibres are present in the trigeminal nerve.

SUMMARY

1. Several ganglia are found in that part of the internal carotid plexus which passes through the cavernous sinus.

2. The ganglia are close to the abducent nerve.

3. In the ganglia are found a mixture of round pale and multipolar dark cells.

4. The ganglia are in immediate connection with the unmyelinated fibres, and are probably sympathetic in nature.

5. Unmyelinated fibres arising from the ganglia, together with fibres of the internal carotid plexus enter the ophthalmic nerve.

CONTRASTING TYPES OF AUSTRALIAN SKULLS

By FREDERIC WOOD-JONES
Melbourne

Attention has been drawn elsewhere (1) to the fact that in every large series of skulls of Australian aborigines a number of unusually small female crania is to be expected.

The failure to recognise that this small-headed female element forms a normal constituent of the population has already produced a certain amount of confusion in the literature of Australian physical anthropology.

But just as these small females are to be expected in any large collection, so too are a certain number of crania showing exaggerated masculine characters combined with unusually large size. These almost outlandish male skulls are remarkable for their highly developed sexual and racial characters. The jaws and teeth are of great size, the brow ridges are enormous and the skull in general attains to a massiveness and ruggedness that was termed "Neanderthaloid" by Burkitt and Hunter (2). As a rule the skull bones are remarkably thick and heavy, and in every way these crania display in an exaggerated manner those features that we are accustomed to associate with the typical male Australian skull. Skulls of this type have been described by Flower (3), Barnard Davis (4), Burkitt and other anthropologists, and the skull of "King Jimmy of the Mordialloc Tribe" figured by Halford (5) was obviously a member of this class. Of his illustration Halford says that it depicts a skull "which in the original was even more brutal than is here represented," and in norma lateralis it presents a very close approximation to the characters of the skull illustrated here in figs. 3 and 4. These skulls are found in collections made in all parts of Australia, and of the ten that I have selected as especially illustrating their characters, one comes from Western Australia, one from Northern Australia, one from Wentworth, one from Central Australia, one from New South Wales, two from Victoria and three from South Australia. Of these ten large male skulls the average and maximum measurements are as follows:

	Average	Maximum
Maximum length (1 A)	196·5 mm.	215 mm.
Maximum breadth (1 A)	132·2 mm.	143 mm.
Basi-bregmatic height (1 A)	137·0 mm.	143 mm.
Schmidt's cranial modulus	155·5	163·3
Cranial capacity (measured)	1334·5 c.c.	1470 c.c.

These measurements stand in marked contrast to those of ten small, but fully adult, female skulls whose measurements are given below:

	Average	Minimum
Maximum length (1 A)	168·3 mm.	160 mm.
Maximum breadth (1 A)	119·9 mm.	116 mm.
Basi-bregmatic height (1 A)	119·2 mm.	115 mm.
Schmidt's cranial modulus	135·7	132·2
Cranial capacity (measured)	940 c.c.	855 c.c.

In order to give an idea of the extreme contrast that may be present between the outlandish masculine skull and the small feminine skull, I have superimposed the diopterographic tracings of two skulls, the female from South Australia and the male from Wentworth (see fig. 1). The principal measurements of these two skulls are as follows:

	Male	Female
Maximum length	215	160
Maximum breadth	132	116
Minimum frontal breadth	101	87
Basi-bregmatic height	143	121
Auriculo-bregmatic height	123	103
Nasio-basilar length	112	92
Basi-alveolar length	122	98
Naso-alveolar height	79	59
Maximum bi-zygomatic breadth	143	118
Palate breadth	73	63
Palate length	74	57

The small female skull (for which I am indebted to Dr Angas Johnson of Adelaide) furnishes a basis for estimating such peculiarities as may distinguish the so-called "Jervois" skull. This skull was found in Central Australia in 1929 and, although it was claimed as possessing "the lowest known cubic capacity of any complete human skull," it has not so far been figured or described. For a loan of a cast of this incomplete skull I am indebted to Mr Gilbert Rigg, who was instrumental in the finding of the original. The principal measurements of this cast are:

Maximum length	174 mm.
Maximum breadth	128 mm.
Basi-bregmatic height	116 mm.
Schmidt's cranial modulus	139·3
Cranial capacity (measured by Sir Colin MacKenzie) between 956 and 980 c.c.	

In order to show the position of the "Jervois" skull in the series of small-headed Australian females, the diopterographic drawing of its cast has been superimposed upon that of the small South Australian skull in fig. 2. It will be noticed that, with the single exception of the basi-bregmatic height, the South Australian female is considerably smaller than the "Jervois" skull. Although Sir Colin Mackenzie originally stated that the "Jervois" skull was more ancient than *Sinanthropus*, he has apparently abandoned all claims for its antiquity, and the skull may be dismissed from further discussion.

The large male skull from Wentworth (for which I am indebted to Dr Rowden White of Melbourne) provides an excellent basis by which to estimate the characters of other outlandish Australian male skulls. Concerning this skull there is no question of antiquity involved. It is indubitably that of a recent Wentworth native, and its characters are merely those of the ordinary male

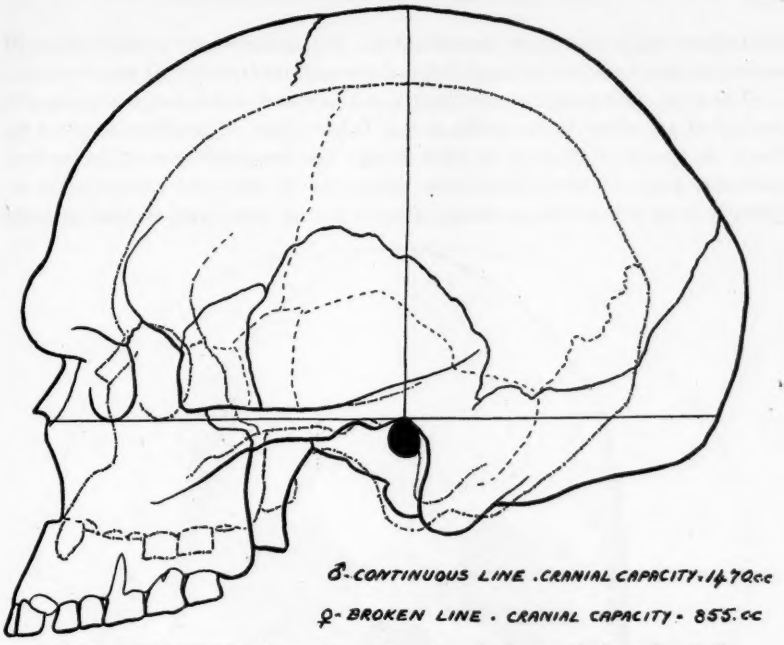

Fig. 1. Superimposed outlines of a small female and a large male Australian skull. Half natural size.

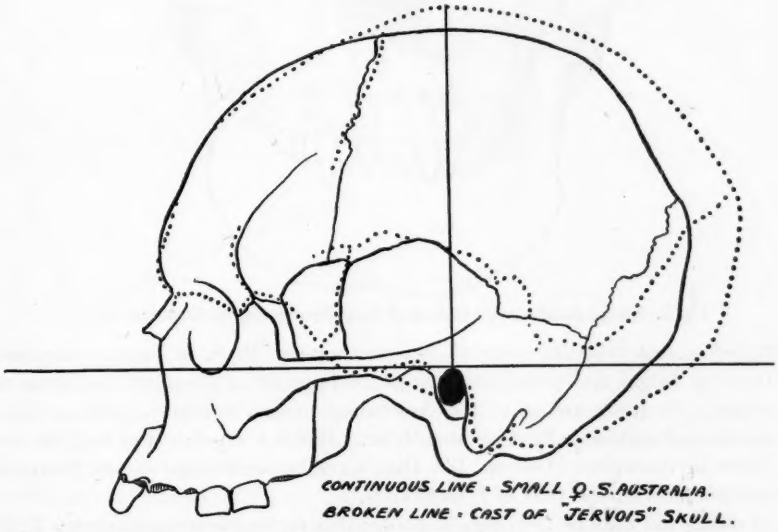

Fig. 2. Superimposed outlines of the small South Australian skull and the "Jervois" cast. Half natural size.

Australian skull somewhat accentuated. Its features are sufficiently well shown in figs. 3 and 4, and any detailed description is rendered unnecessary.

The only skull that has ever been described and which has any claims to geological antiquity in Australia is the Talgai skull, originally described by Dr S. A. Smith of Sydney in 1917–18 (6). The circumstances of its finding, however, preclude any real reliance being placed upon the evidence for regarding it as other than a comparatively recent skull, and its claims must

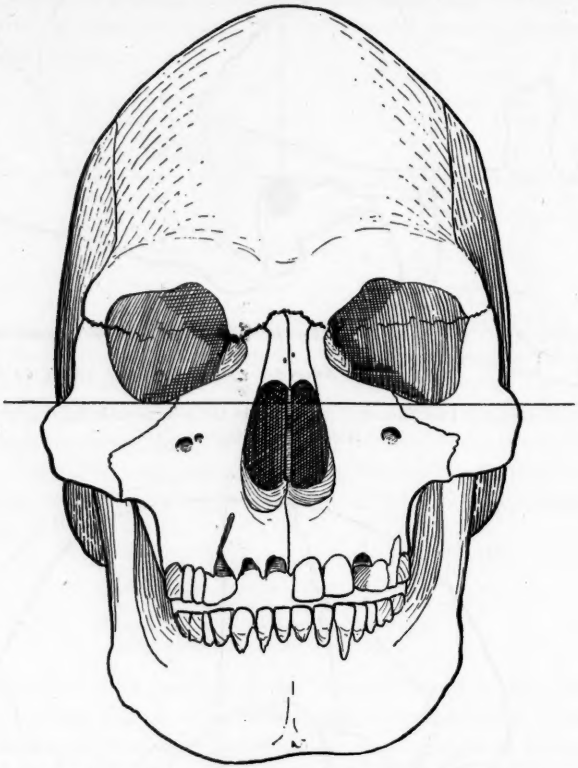

Fig. 3. Norma facialis, large male skull from Wentworth. Half natural size.

therefore rest upon its morphological characters. Dr S. A. Smith recognised that the Talgai skull presented "the general picture of a cranium similar in all respects to the cranium of the Australian to-day, combined with a facial skeleton of undoubtedly Australian type." But in the palate and teeth he saw "certain characters more ape-like than have been observed in any living or extinct race, except that of *Eoanthropus*."

Since the date of the original publication further investigations by T. D. Campbell (7) and by Burkitt (8) have rightly tended to diminish the importance

of certain features that were taken by Smith to indicate a peculiarly ape-like dentition: and to-day it is fair to say that the Talgai skull should be regarded as that of a young aboriginal with a large palate and large teeth, but still not wholly outlandish even in regard to these features.

Fig. 5 shows the outline of the cast of the Talgai skull superimposed upon the outline of the recent Wentworth skull, and it is suggested that, despite the distortion which the former has undergone, the changes brought about by the

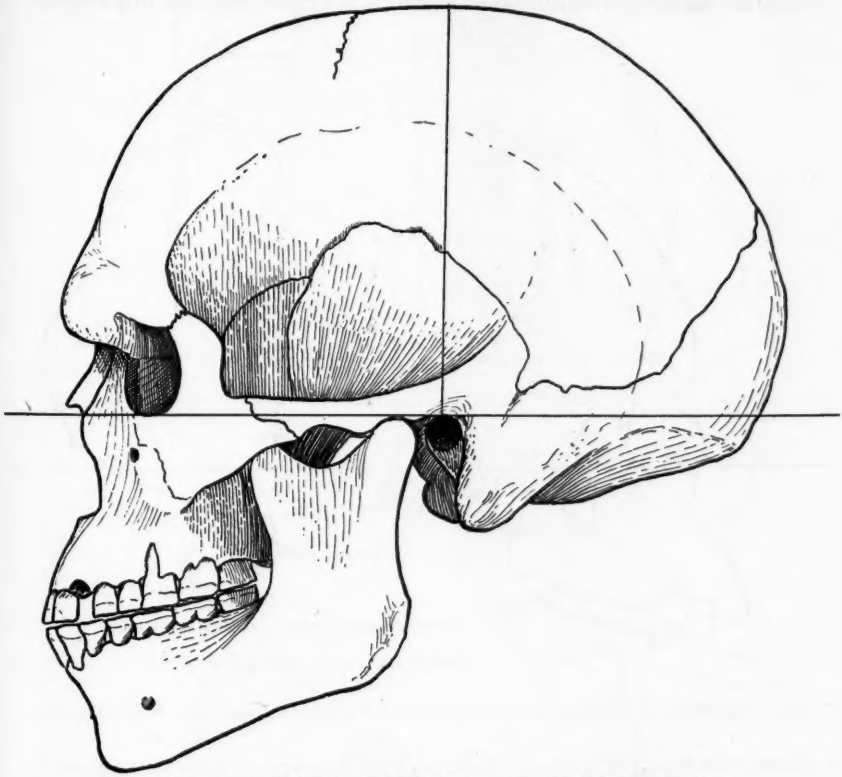

Fig. 4. Norma lateralis, large male skull from Wentworth. Half natural size

completion of growth and eruption of the third molars in the Wentworth skull are such as one would have expected in the adult Talgai individual.

Since the distinction of the Talgai skull admittedly lies only in the palate and teeth, diopterographic drawings of the modern Wentworth and of the Talgai palates are reproduced in figs. 6 and 7. The teeth of the Wentworth skull are excessively worn and the canines are absent, but even with this disadvantage it clearly demonstrates the fact that the Talgai skull has no real claims to be considered as being outside the range of variation of the recent aboriginal.

Although the so-called "Cohuna" skull was obtained in 1925 and enjoyed considerable notoriety in the daily press, no description of it has ever been published by Sir Colin Mackenzie, in whose possession it is. It is much to be regretted that no measurements, illustrations or casts of this skull have ever been made available to physical anthropologists, for, since all the circumstances of its finding point to its being a recent skull, its claims must rest on its morphological characters alone. In all probability it is but little different in its essential characters from the Wentworth skull figured here, and other recent

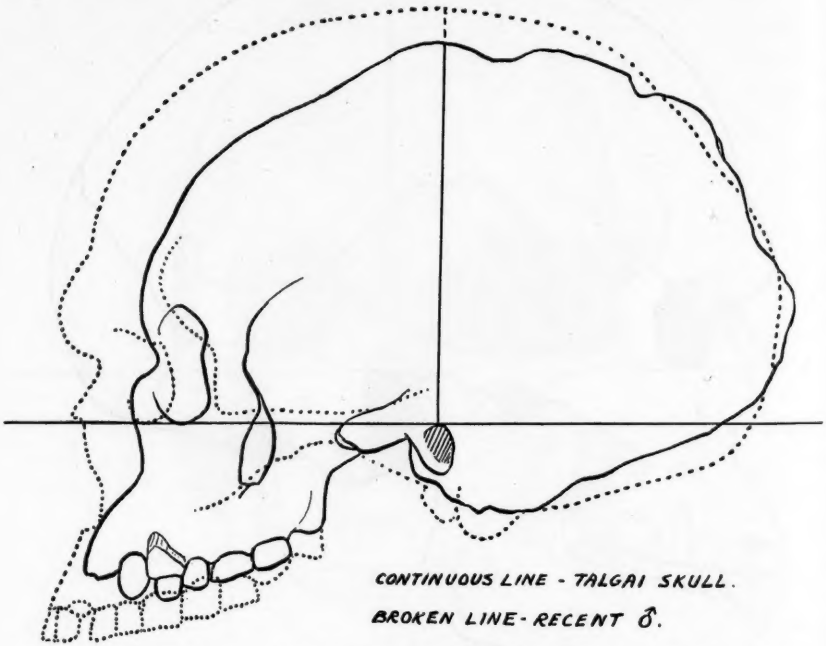

Fig. 5. Superimposed outlines of the large Wentworth skull and the Talgai cast. Half natural size.

skulls of its type. In the meanwhile, pending its proper description, it must be relegated to Prof. Boule's class of anthropological "bric-à-brac."

The fact that both the Talgai and the "Cohuna" skulls are mineralised carries but little weight in favour of their geological antiquity. Mineralised human skulls, unearthed in situations which altogether preclude any possibilities of real antiquity, are of frequent occurrence in certain districts in Australia. One such skull from the Murray basin in the neighbourhood of Cohuna was submitted to analysis in order to determine how much organic matter remained in the bone. The skull was that of a perfectly normal aboriginal type. The analysis was carried out for me by the late Dr Heber Green. His

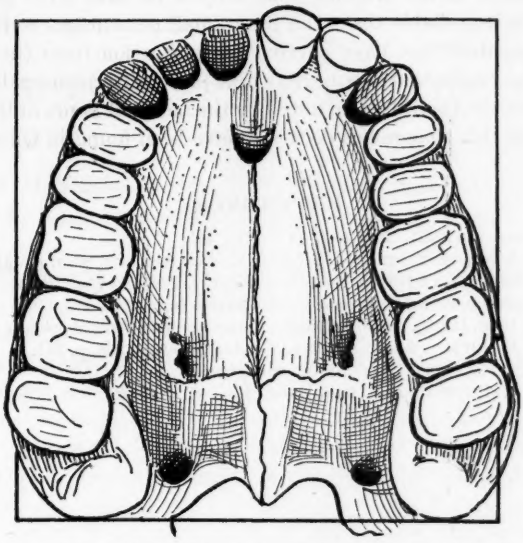

Fig. 6. Diopterographic drawing of the palate of the large Wentworth skull. Natural size.

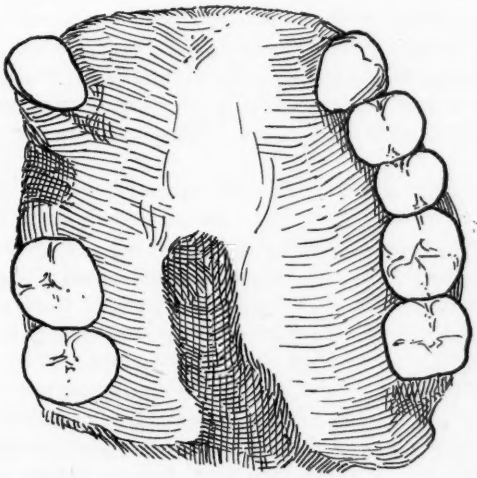

Fig. 7. Diopterographic drawing of the palate of the Talgai cast. Natural size.

report states that "of the 10 per cent. fats and 50 per cent. organic matters probably present in the original skull, only 0·032 and 0·155 per cent. now remain, and it is probable that even these small percentages were not derived from the bone itself but have entered by infiltration from the surrounding soil." That mineralisation of bone may take place with considerable rapidity in certain districts in Australia is attested by the fact that bones of the introduced horse in which this change has occurred have been found in Queensland.

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VARIATIONS IN THE LOWER END OF FEMUR FROM INDIANS

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Certain conclusions have been drawn from the variations found in the lower end of femur after a comparative study of bones from modern and certain primitive races.

The results published by Martin (1) were based on the examination of femora of modern English and Irish (75) and a number of other types (in all 168). The principal causal factor in explaining the variations has been the squatting posture. The figures for the modern non-squatting and the primitive squatting races show definite differences, and it is the object of this study to obtain figures from the examination of Indian femora to see if they correspond to the published results. From what follows it will be seen that such is the case.

The investigation was carried out on the material available at the King George's Medical College Anatomy Department. The bodies that come for dissection in the Department are the unclaimed ones, and the social condition of the province is such that it leaves no doubt that they belonged to the economically poorer class. These people are hard-working labourers and squatting is the posture they adopt both for rest and work.

We might expect variations in all the elements constituting the joint between squatters who keep the knee joints in continued acute flexion and non-squatters in whom such a posture is occasional and rarely maintained for long.

To appreciate the significance of these differences preparations of forty-six freshly dissected joints were examined. The soft parts were removed and the joint area left intact. The knee joint was first opened from in front by turning down the patella with its tendon and snipping across the ligamentum mucosum to expose the anterior cruciate ligament. The joint was later opened from behind by dissecting away the capsule and the pad of fat to expose the posterior cruciate ligament. The relation of the two ligaments to the lower end of the femur during the various phases of joint movement was then studied.

The results of the study can be summarised thus:

The arrangement of the cruciate ligaments is such that when the knee joint is examined in a freshly opened state two interligamentous fossae may be defined which are converted into osseo-ligamentous canals for the lodgement of the ligaments during the extremes of flexion and extension alternately.

Anterior intercrucial fossa

With the joints flexed at right angles the two ligaments are crossing nearly half-way and from in front, as shown in fig. 1, a fossa, whose floor is formed by synovial membrane covering the whole of the anterior surface of anterior cruciate and the anterior half of the posterior cruciate ligaments, and bounded on the sides and front by the edge of articular surface, is brought into view. A cavity protrudes in the form of an interligamentous bursa to facilitate the scissor action.

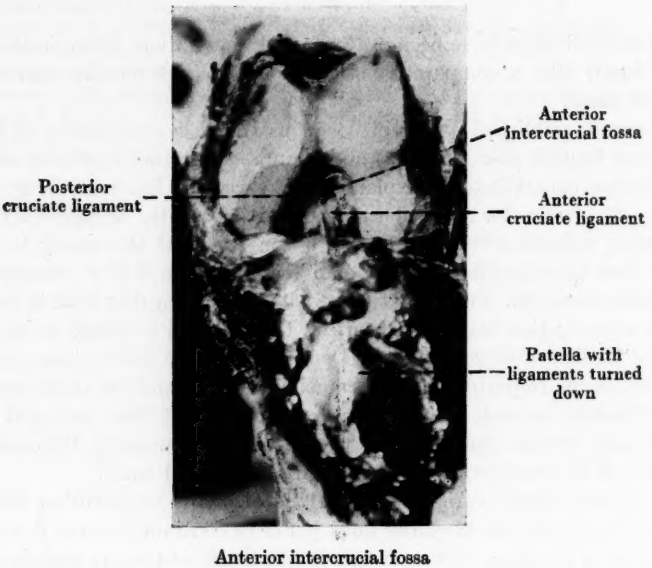


Fig. 1. The joint from in front after turning down the patella and snipping across the ligamentum mucosum.

As the joint is passively extended the fossa may be seen to be gradually obliterated by the approximation of the ligaments until it is reduced to an osseo-ligamentous canal, bounded laterally and in front by the articular border and medially by the posterior cruciate ligament.

Finally in full extension this canal is completely obliterated by the lodgement of anterior cruciate ligament which is now tight and resting directly against the edge of articular patellar surfaces, as shown in fig. 2. The pressure of the anterior cruciate ligament at this point has a marked effect on the configuration of the lower end of the femur which is noticeable both in freshly macerated and dried bones.

The posterior intercrucial fossa

With the exposure of joint from behind, as shown below, a fossa bounded laterally by the extrasynovial surface of the posterior limb of the anterior cruciate ligament, medially by the lateral surface of medial condyle and superiorly and in front by the anteromedial quadrant of intercondyloid fossa and inferiorly by the extrasynovial surface of posterior cruciate is defined. Under natural conditions it is a closed cavity roofed over by the capsule and completely filled up with easily displaceable soft fat.

Fig. 2.

Fig. 3.

Fig. 2. Showing anterior cruciate ligament abutting against the articular edge of femur during extension.

Fig. 3. The arrow pointing to the lateral part, the place of pressure by the anterior cruciate ligament during extension, being deeper than the medial.

With the joint flexed to a right angle, this fossa is converted into a posterior osseo-ligamentous canal by the approximation of the post-cruciate ligament towards the intercondylar fossa on the medial side of the anterior cruciate ligament, under natural conditions the soft fat having been displaced posteriorly against the relaxed capsule.

With the joint acutely flexed the canal is obliterated by the lodgement of the ligament which is now abutting tight against the medial half of intercondyloid ridge.

In fig. 4 it will be seen that the ligament of Wrisberg stretching tightly

across the posterior cruciate ligament is the first to come in contact with the intercondyloid ridge.

This pressure of the ligament has a similar influence on the ridge as that of the anterior cruciate on the patellar border, and the result can be seen well marked both in the recent and dried specimens.

The two effects as shown in figs. 3 and 5, brought about by the anterior and posterior cruciate ligaments during acute extension and flexion respectively, will vary to a large extent with the range of movement through which the

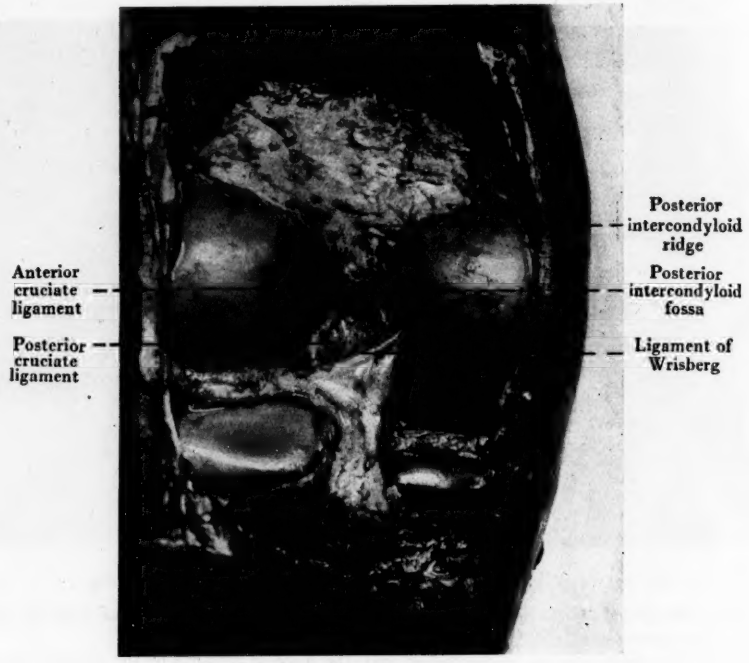


Fig. 4. Showing the posterior intercrucial fossa.

joint is put. The latter depends to a large extent on the person's occupation and mode of life.

Taking the case of the posterior cruciate ligament only, if the occupation and mode of life were such as is the case of Indians who use the joint in a markedly flexed condition, we would expect an exaggerated concavity at the place of contact on the intercondyloid ridge. In modern European races whose occupation and mode of life do not necessitate such an extreme range of long-maintained flexion, this effect would not occur.

Not only will the posterior cruciate cause a grooving of the intercondyloid

ridge in Indian femora but will also cause an increase in depth of the intercondyloid fossa at that level.

To test the accuracy of this statement 200 femora, obtained from bodies coming to the Dissection Hall, were chosen and subjected to a systematic examination.

The intercondyloid ridge showed a definite concavity and upward grooving at the contact point in practically all the femora examined, bearing out the above view as shown in fig. 5.

The depth of the intercondyloid fossa at the level of the groove and the height of the articular surface were measured in the same way as that adopted

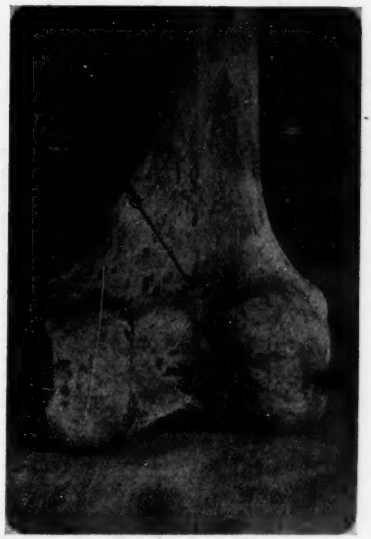


Fig. 5. The intercondyloid ridge is markedly concave at the point of contact of posterior cruciate ligament pointed by the arrow.

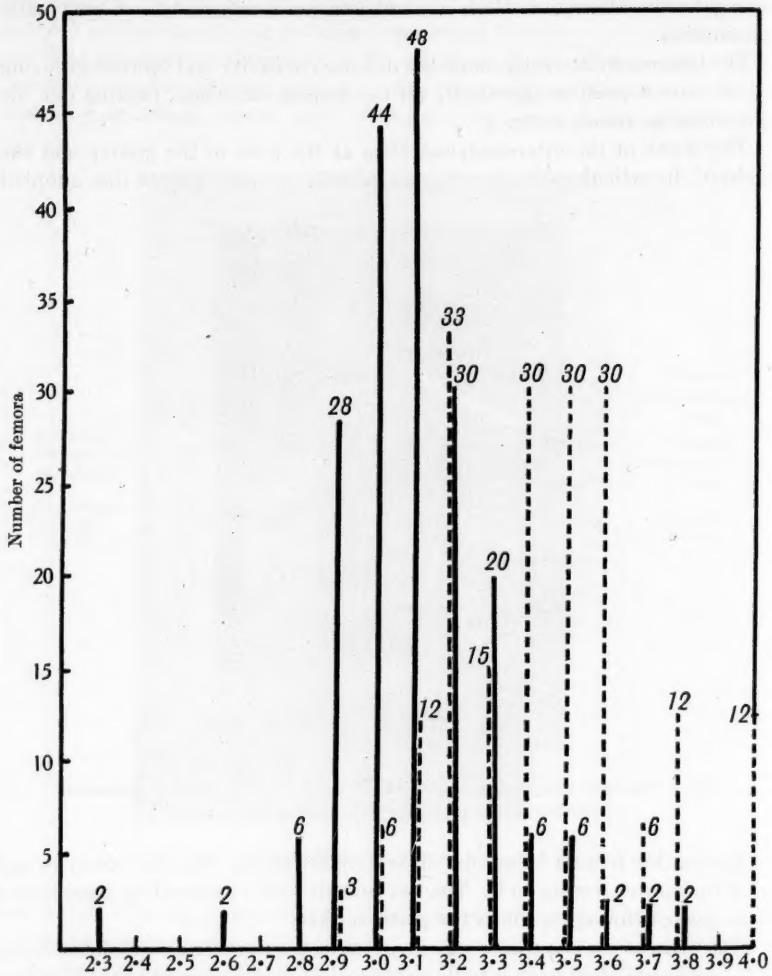
by Martin, the femora being placed on a plane surface with the condyles and great trochanter resting on it. The two heights were measured by a graduated probe passed through a slit in the plane surface.

The ratio of the two measurements, that is, the number by which the depth of the intercondyloid fossa is to be multiplied to give the height of the articular surface was tabulated as shown in Table I.

Table I shows that, although the figures range from 2·3 to 3·8, the majority (85 per cent.) of Indian femora fall between 2·9 to 3·3.

Table I also shows the comparison of Indian femora with those of modern Irish, the figures used for the latter being based on the published results of Martin for 63 bones measured in the same way.

Table I. *Distribution of femora in Indians as compared to modern Irish.*



Number by which depth of fossa must be multiplied to equal anteroposterior depth of articular surface.

——— Indian.
------ Modern Irish.

The modern Irish were chosen for comparison since Martin's investigations showed that their femora were on the whole those of a non-squatting people. According to expectations the table very clearly shows that the intercondyloid fossa is remarkably shallower in the Irish and deeper in the case of Indian femora. This is in agreement with the explanation given with regard to the position of posterior cruciate ligament during acute flexion.

Inspection of the table shows that as the figures go below 3·3 the chances of the femur being that of a squatter increases while above 3·3 it is more likely to belong to a non-squatter.

CONCLUSIONS

1. 200 femora from Indian bodies have been investigated with a view to note the effect of posterior cruciate ligament on the intercondyloid ridge and to determine the depth of intercondyloid fossa.

2. Series of knee joint preparations have been examined to note the relation and effect of posterior cruciate ligament on the intercondyloid ridge during acute flexion.

3. In the femora of squatting people the intercondylar line is in the majority of cases crossed by a distinct groove for the post-cruciate ligament.

4. The depth of intercondylar fossa is greater in the femora of squatters than it is in those of non-squatters, and that its cause is due to the pressure by the post-cruciate ligament when the joint is fully flexed as in squatting.

5. The last two conclusions are in agreement with those arrived at by Martin.

6. The ratio between the depth of the intercondyloid fossa and the height of the articular surface is such that in non-squatters it tends to rise above and in squatters fall below 3·3.

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FURTHER OBSERVATIONS ON THE VENAE CAVAE OF CERTAIN MAMMALS

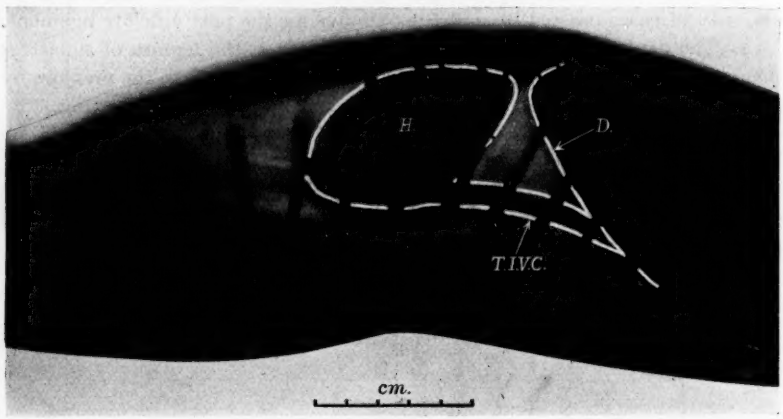
By K. J. FRANKLIN, D.M.

University Department of Pharmacology, Oxford

I. THE LIE OF THE HEART AND OF THE THORACIC INFERIOR VENA CAVA OF THE CAT IN THE SUPINE POSITION

The normal lie of the venae cavae of the cat in the prone position has been described and pictured in a previous number of this *Journal* ((1), pp. 605–6). As the majority of cats used in physiological experiments are placed in the supine position, it was thought advisable to examine the lie of the thoracic viscera in this position also, and to see what changes, if any, occurred.

A female cat, weighing 2940 gm. and having a "snout-buttock" length of 56 cm., was anaesthetised with ether and chloroform, and tied on to a board in



Text-fig. 1. X-ray photograph of a cat in the supine position. *H.* heart; *T.I.V.C.* thoracic inferior vena cava; *D.* rostral edge of diaphragm shadow.

the supine position with its limbs extended. It was then screened. On the X-ray screen the diaphragm could be seen to move above 8 or 10 mm. in inspiration, and the caudal part of the sternum was pulled inwards a little by the contraction of the muscle. The breathing was almost entirely diaphragmatic, the abdominal wall relaxing *pari passu* with the contraction of the diaphragm. The heart remained close up against the sternum despite the supine position; it also moved caudally about 2 mm. in inspiration, and the trachea apparently lengthened a corresponding amount. The caudal movement

of the heart in inspiration in this species gives a reason for the presence of spiral collagen fibres in the superior vena cava ((1), p. 604; (2), pp. 384–5), and the greater lengthening of the thoracic inferior vena cava explains why the spirals are more marked a feature of this vein than of the superior vena cava. The photograph reproduced here (text-fig. 1) was taken when expiration was practically complete.

The cat was afterwards shot with the humane killer and left to become rigid in the supine position, the lungs being moderately distended through a tube tied into the trachea. When the thorax was opened later by a right paramedian incision, it was clear that the lungs were the agents responsible for keeping the heart up against the sternum in the supine position, for the heart and venae cavae dropped over a centimetre on deflation of the lungs; the pleuro-pericardial membrane which connects the heart and venae cavae to the sternum and diaphragm was powerless to prevent this drop.

II. AN ACTION OF THE DIAPHRAGM UPON THE THORACIC INFERIOR VENA CAVA OF SOME MAMMALS

An X-ray film, kindly made for the writer by Dr Robert Janker (of the Röntgeninstitut der chirurgischen Universitäts-klinik und-Poliklinik, Bonn), showed very conclusively that the volume of the thoracic inferior vena cava of the cat diminishes in inspiration (3). The writer has described one factor, a structural one, which would contribute towards this action, and which is by itself more powerful than the inspiratory diminution of pressure within the mediastinum (3). But in some Mammals there is another intrathoracic factor which may help, for a band of muscle fibres from the sternocostal portion of the diaphragm often loops over the thoracic inferior vena cava at the caval foramen, and compresses the vein when the diaphragm contracts. This "caval band" was mentioned earlier in this *Journal* ((2), pp. 385–6), and has been seen in several dogs since then; in one dog it produced a marked indentation of the vein in inspiration. It is not, however, muscular for the whole of its course in all dogs, and the effect upon the vein is roughly proportional to the amount of muscle in any particular animal.

The analysis of so rapid an action had necessarily to be made by cinematographic means. Films were made of one cat, five dogs, and two rabbits. In all cases the animals were given a preliminary subcutaneous injection of atropine sulphate. The cat and the dogs were thereafter anaesthetised with ether and chloroform, and a cannula inserted into a leg vein. Through this Nembutal veterinary solution was injected, in the dosage of 1 c.c. per 5 lb. body weight, over a period of 8 min., the general anaesthetic being discontinued after the first 3 or 4 min. of the injection of the narcotic solution. A tracheal tube was then inserted, and artificial respiration was given until a large portion of the right thoracic wall had been removed. During the photography the artificial respiration was stopped and this caused the contractions of the diaphragm to

recommence. The rabbits were kept under general anaesthesia without Nembutal.

In the cat and in the dogs the general effect of the "caval band" was similar, though it was best seen in the cat (Plate I). The band compressed the thoracic inferior vena cava in inspiration, and at the same time this vein was lengthened, flattened and narrowed by the excursion of the diaphragm as a whole. The films leave no doubt in one's mind about the action of the "caval band," and it may provisionally be presumed to have such an effect in any Mammals in which it is found to be present. In the rabbits there was no such band; but some more or less longitudinally coursing bundles of collagen fibres, which passed from the spinal portion of the diaphragm on to the upper surface of the vein, caused some flattening of it in inspiration.

The next work on the effects of respiration on the inferior vena cava will be an examination of the intrahepatic portion of the vessel. This will be made, it is hoped, by means of X-ray cinematography combined with injections of X-ray opaque substance into the femoral vein.

CONCLUSION

1. The lie of the heart and great veins in the cat is unaffected by change from the prone to the supine position.

2. A band of diaphragmatic muscle loops over the thoracic inferior vena cava in some Mammals, and has been shown by cinematographic records to compress this vein in inspiration.

The present work forms part of a study of the venous return in Mammals, the expenses of which have been defrayed by a generous grant from the Rockefeller Foundation.

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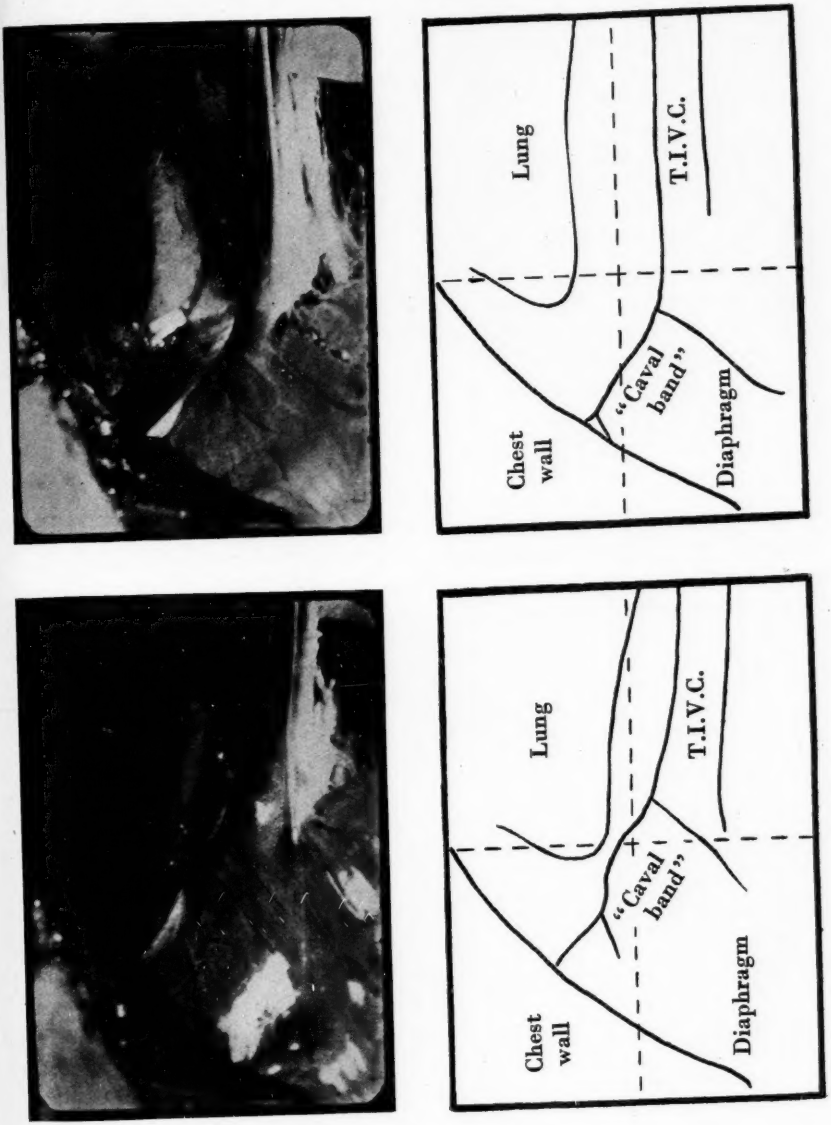
EXPLANATION OF PLATE I

Cinematographic pictures and explanatory diagrams of the action of the "caval band" in the cat. A large portion of the right thoracic wall has been removed. On the left, expiration; on the right, inspiration. *T.I.V.C.* thoracic inferior vena cava.



FRANKLIN—Observations on the Venae Cavae of certain Mammals

A CASE OF ABNORMALITY IN THE VENOUS SYSTEM OF THE COMMON FROG (*RANA TEMPORARIA*)

By A. J. GROVE, M.A., D.Sc. and G. E. NEWELL, B.Sc.
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This specimen was one provided for ordinary class work, and, so far as could be judged externally, was perfectly normal. It appeared to be a quite healthy mature male. The abnormal character of the specimen was not discovered until the student had carried out the preliminary operations of opening the body and removing the middle portion of the pectoral girdle to expose the heart. After this, all dissection was carried out by ourselves.

The appearance of the venous system, as first seen, is shown in fig. 1, from which it will be clear that the right anterior vena cava is absent, and there

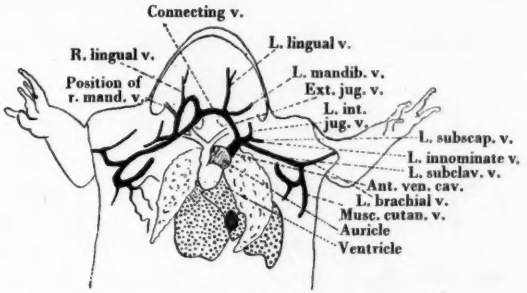

Fig. 1.

appears to be only one auricle (the left). To compensate for the absence of the right anterior vena cava, a connecting vessel passes from the left external jugular across the floor of the pharynx to the right side of the body. This appears to pass to the point of junction of the external jugular, innominate and subclavian veins of the right side. In addition, however, a second fairly large connecting vessel joins the right lingual vein with the main connecting vessel, forming a loop in this region.

On the left side, the secondary vessels, lingual, mandibular, internal jugular, subscapular, brachial and musculo-cutaneous veins are normal, and the corresponding veins on the right side are approximately symmetrical with them, with the possible exception of the right mandibular vein, which could not be detected with certainty owing to the absence of blood. A strand of pigmented tissue which may have represented this vessel was present in the appropriate position.

The completion of the removal of the pericardium enabled a closer examination of the sinus venosus and the pulmonary veins to be made. The normal triangular shape of the sinus venosus was, of course, altered by the absence of the right anterior vena cava, but the most remarkable feature was that the common pulmonary vein formed by the junction of the right and left pulmonary veins apparently entered the sinus venosus near the middle line at about the termination of the posterior vena cava (see figs. 2 and 3). At this

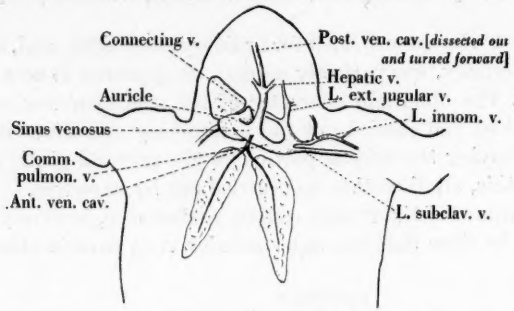

Fig. 2. The heart has been turned forward to show its dorsal surface.

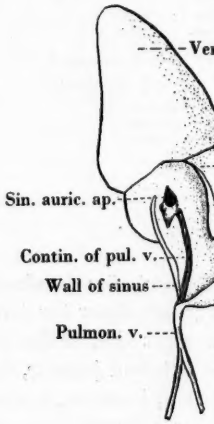

Fig. 4.

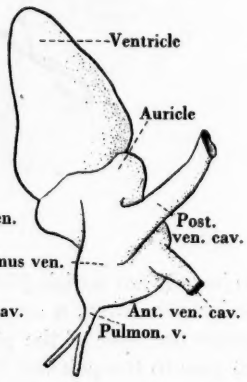

Fig. 3.

stage of the dissection it was obviously of importance to determine whether the pulmonary vein opened directly into the sinus venosus or passed through it to the heart. A fine black bristle was introduced into the common pulmonary vein and then the dorsal wall of the sinus venosus was laid open, when it was found that the bristle was still enclosed within a continuation of the pulmonary vein (fig. 4). This continuation terminated at the left side of the sino-auricular aperture

The incision in the dorsal wall of the sinus venosus was then continued into the auricle and it was found that, although externally there appeared to be only one auricle (the left), it was divided by a thin membranous septum into left and right halves. This septum passed from the sino-auricular aperture to the auriculo-ventricular aperture, dividing it into two (fig. 5), and projecting through it into the ventricle. The pulmonary vein lay to the left side of this septum projecting into the sino-auricular aperture. The auriculo-ventricular aperture was guarded by the usual two valves. The condition of the truncus arteriosus was normal.

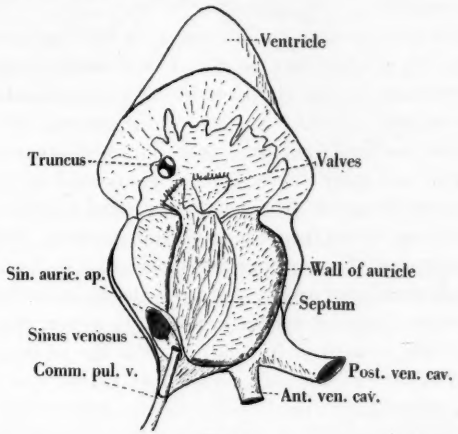

Fig. 5.

DISCUSSION

The recorded cases of abnormalities in the vascular system of the *Anura* have been admirably summarised by O'Donoghue (1931). The case under consideration approaches nearest to the arrangement of the veins in example 7 (p. 190), but there are, however, some points of difference. In the figure given, the anastomosing vessel joins the two external jugular veins, and the additional connecting vessel enters the right external jugular at about midway along its length. In our specimen, however, the anastomosing vessel passes from the distal end of the left external jugular to the point of junction of the right external jugular, innominate and subclavian veins, and the connecting loop passes from about the middle of the anastomosing vessel to the right lingual vein.

No mention is made by O'Donoghue of the relation of the pulmonary vein to the heart. From the figure, two auricles appear to be present so that it is to be assumed that the position and condition of the pulmonary vein is normal. The only case cited by O'Donoghue in which the pulmonary vein appears to enter the sinus venosus is example 2 (p. 183) recorded by Lyle (1899), but this case is totally different in other respects. O'Donoghue assumes

in this particular case that the normal separation of the blood streams is upset. There is, however, no indication that the actual opening of the pulmonary vein was determined. This is unfortunate, because in the specimen we have described the external appearance was that of the pulmonary vein entering the sinus venosus, but further dissection showed that it passed right through the sinus. This at once recalls the condition found in the *Dipnoi*, in which the pulmonary vein passes through the sinus venosus and discharges its blood into the left side of the incompletely divided atrium (Goodrich, 1930, pp. 449–50). But here again the conditions are not exactly the same, for in our specimen the septum is complete.

The chief point of interest in connection with this frog is the consideration of when and how this abnormality arose; an abnormality which has evidently arisen from the absence of the right cuvierian sinus since the right anterior vena cava was entirely absent. In the young embryo the venous system appears as anterior cardinal veins and posterior cardinal veins lying laterally in the body wall, and later these become connected to the heart by the cuvierian sinuses which apparently are derived from a plexus of blood vessels lying in the mesoderm of the future septum transversum. It is of interest and importance to note that this region affords the usual route by which a transversely orientated vessel can arise connecting the heart with the vessels lying lateral to the coelom. It must not be forgotten, however, that associated with the formation of the structures in relation with the pharynx, the coelom is early obliterated in that region and, consequently, this also affords a possible region in which connecting vessels between the lateral ones might develop. It is also of importance in this connection that the external jugular and its related vessels develop independently of the primordial lateral vessels. Therefore it is not unreasonable to postulate that in the event of one cuvierian sinus failing to develop, this is counterbalanced by the establishing of a connecting vessel between the jugular veins, or in that region, thus enabling all the systemic blood to be returned to the heart. This explanation is supported by the comparable examples given by O'Donoghue, for in every case where the vena cava is absent, in part or entirely, the connecting vessel is developed in some part of this region.

A still more striking thing, however, is that in every case it is the *right* anterior vena cava which is absent or defective. What possible factor could produce this abnormal condition so consistently? There appear to be two possibilities. Either the cuvierian sinus was formed and obliterated early, or else its complete formation never took place. The curvature of the embryo within the vitelline membrane might explain the partial or complete occlusion and subsequent obliteration of the cuvierian sinus on one side, but why always the right side is not evident. An examination of about twenty-five preserved embryos showed roughly equal numbers curving to the right and left. It is possible that closer examination of living material might throw some light upon this point, but such material is not available just now.

Curiously enough, whilst this investigation was in progress, a second frog turned up in the class showing a closely similar condition. As the figure (fig. 6) shows, the only points of difference are the course of the anastomosing vessel (from the point of junction of the left external jugular, innominate and

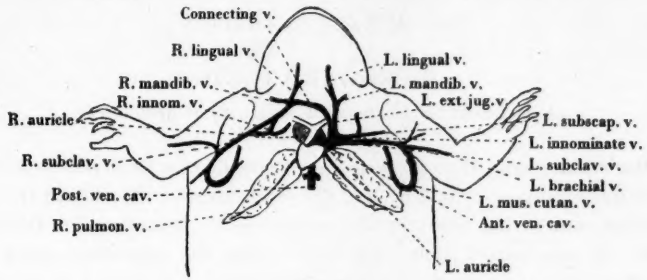

Fig. 6.

subclavian veins to the distal end of the right external jugular); the absence of a secondary loop and the appearance externally of right and left auricles. Also, each pulmonary vein receives a branch from the oesophagus. In other respects the course of the common pulmonary vein and its relation to the sinus venosus is as in the previously described example.

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A NOTE ON THE STERNAL GLAND OF *MYRMECOBIUS*

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The Marsupial genus *Myrmecobius* was established by Waterhouse in 1836 (1), and was more fully described by him ten years later (2). Neither in the generic description, nor in his account of the species *M. fasciatus*, did Waterhouse mention the specialised skin area that marks the cutaneous chest gland. Beddard in 1887 (3) gave a description of the gland and figured its microscopic structure, and, according to his findings, the gland was a far more complex structure than are those found in nearly similar situations in many other Marsupials. In addition to the ordinary dermal glandular structures, Beddard described and figured a deep, subcutaneous, glandular mass unrepresented in the typical skin gland of other Marsupials. In 1888 Oldfield Thomas (4) incorporated a résumé of Beddard's description of the pectoral gland into the definition of the genus and included the criterion: "chest with a peculiar complex gland, opening on the surface by several large and distinct apertures," as a generic description. This generic character has been followed by all subsequent writers, but Cabrera (5) is rather more guarded in that he only claims the presence of "una glandula que se abre al exterior por varios orificios relativement grandes" as a distinction of the family Myrmecobiidae.

Since some sort of dermal sternal or pectoral gland is of such frequent occurrence in Marsupials, it was considered advisable to re-examine *Myrmecobius* in order to ascertain if the gland in this animal differed from the typical form by possessing a large and specialised subcutaneous element.

In the adult of both sexes there is, over the sternal region, at the junction of the neck and thorax, an area possessing peculiar characteristics. This glandular area is rounded in outline and has a diameter of about 10 mm. Its surface, which is slightly raised above the level of the surrounding skin, is practically hairless, coarsely roughened, and pigmented in different specimens from light grey to sooty black. Irregularly scattered over it are a number of openings of various sizes, the largest being about 1 mm. in diameter. Beddard showed that this peculiar area of skin was associated with various underlying glandular structures, and he described four distinct types of gland situated beneath the pigmented skin (see fig. 1). These different types of glands described by Beddard were: (1) sebaceous glands situated in relation to the sparsely scattered hair follicles, and mainly round the periphery of the area; (2) sweat glands, opening on the surface, or at the base of (3) large sudoriparous

Fig. 1. Beddard's original figure of the sternal gland. The mass indicated by the letters *gl* is the portion discussed in the present paper. *e*, epidermis; *s*, sweat gland; *d*, its duct; *p*, duct of sweat gland opening into sudoriparous follicle; *f*, sudoriparous follicle; *gl*, compound sweat gland lying below dermal muscles. (Reproduced by permission of the Publication Committee, *Proc. Zool. Soc. Lond.*)

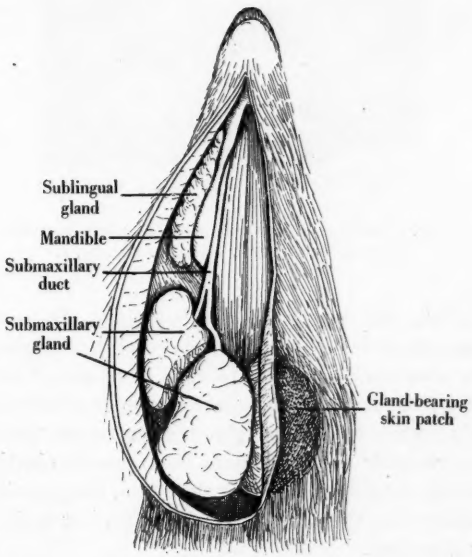

Fig. 2. Dissection of the neck region of *Myrmecobius*.

follicles, the openings of which are visible macroscopically on the surface of the patch; (4) beneath the dermal muscle and subjacent to the foregoing structures a large glandular mass, which was considered to be of the nature of a sweat gland, but for which no duct or openings could be found. It is with this latter structure that this note is concerned.

Dissection of the region deep to the glandular area shows that, lying immediately beneath it and upon the muscles, are bilateral, plate-like, glandular masses, each about 12 mm. in diameter (fig. 2). These are situated upon either side of the mid-line, but the inner thinned margin of the right mass

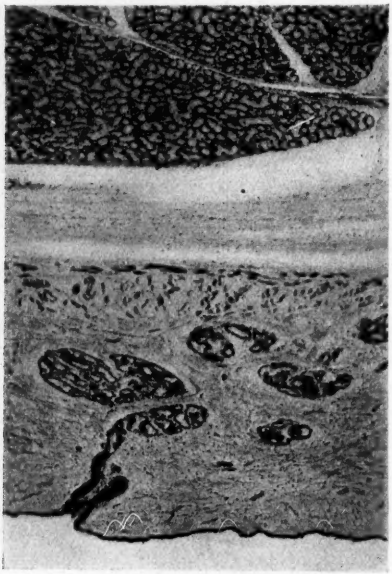

Fig. 3. Section of glandular patch. The deep portion is the salivary gland. Compare with fig. 1.

overlaps that of the left across the median plane. The extremities of the whole gland mass extend for some distance beyond the margins of the overlying skin patch. The anterolateral border of each is separated only by a layer of connective tissue from another and more cranially situated glandular mass. From the anterior extremity of these glands a duct runs cranially to the lateral border of the mylohyoid muscle. There is no communication between this deep gland and the overlying glandular skin area, the prominence of which is due partly to a lens-like thickening of the dermis, but mainly to the bulk of the underlying structure.

Myrmecobius is a specialised ant-eater, and like other ant-eating animals

of every mammalian order, shows remarkable enlargement and caudal extension of the submaxillary salivary glands. Quite obviously the deep gland mass, included by Beddard in his section, and for which he could find no duct, is no part of the dermal gland structure, but is that portion of the complex salivary glands that Leche (6) described as the hinder portion of the divided submaxillary gland. This portion is, in structure, a compound tubular gland of the mucous type. Its structure differs from that of the main portion of the submaxillary gland, the duct of which it joins, for the latter is mainly serous in character (see fig. 3).

Myrmecobius therefore has no distinction among the Marsupials in regard to its sternal gland, since this is of the same sebaceous and sudoriparous type as that familiar in other Marsupial families.

ACKNOWLEDGMENTS

I am indebted to Prof. F. Wood-Jones for furnishing the anatomical material examined.

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A CASE OF MEGALO-DUODENUM WITH VARIOUS VASCULAR ABNORMALITIES

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The following is an account of the anatomical findings in a female child, born in hospital, which from the first day exhibited symptoms of intestinal obstruction, viz. persistent vomiting, passage of stools consisting of mucus only, and increasing jaundice. Laparotomy was performed on the fourth day and revealed complete atresia of the gut in the neighbourhood of the duodenum, but the child's general condition did not admit of further operative procedure. It died the following day. At the post-mortem examination several additional abnormalities were found which we think are worth recording. The abdominal and thoracic contents which had been removed *en bloc*, subsequently came to us for examination. Unfortunately, we had no opportunity of examining the viscera *in situ*.

DESCRIPTION OF SPECIMEN

The specimen consists of the heart and lungs, the whole of the alimentary canal from the cardiac orifice of the stomach to the anal opening, together with the liver, pancreas and spleen. The kidneys and suprarenal glands are also present as well as the bladder and genital organs. The common bile duct is a delicate thread which has been severed proximal to its communication with the intestine; the most careful examination fails to discover its opening into the gut.

The abnormalities found will be divided under two headings: (*a*) Visceral, and (*b*) Vascular.

Visceral abnormalities

The stomach is much dilated, and the lack of any thickening in the pyloric area suggests the absence of a pyloric sphincter. This is confirmed by microscopical examination.

Complete atresia of the gut is present at two points, situated about 2 cm. apart, high up in the small intestine; the intervening portion of the tube possesses a normal lumen. It has been impossible to fix with certainty the anatomical site of these atresiae, because of our failure to locate the orifice of the common bile duct. The opening may have become involved in the atresic area. On the other hand, this region receives several large vessels passing directly from the superior mesenteric artery, which suggests that the area involved is nearer the duodeno-jejunal flexure. Brunner's glands are absent in sections both proximal and distal to the occluded segment.

Below the occlusion the coils of intestine are empty and contracted. Above it the duodenum forms an enormously dilated and hypertrophied S-shaped curve, the proximal loop of which surrounds a small mass of pancreatic tissue; the lower border of the distal loop reaches well below the remaining coils of small intestine, which lie in front of it (fig. 1). That there has been no rotation of the gut is shown by the fact that the caecum, appendix, ascending and

Fig. 1. General view of viscera showing the two atresic areas and the enormously enlarged duodenum with its outline *A, B, C*.

transverse colon lie on the left side of the middle line; secondary fixation has not taken place.

The gall bladder is rudimentary and the common bile duct is severed from its point of attachment to the gut. The upper part of the duct, however, runs behind the first part of the duodenum and enters the right extremity of the transverse fissure of the liver. The spleen is represented by a cluster of nine separate spleniculi, varying in size from that of an almond to that of a millet

seed. One spleniculus is isolated from the others and is adherent to the stomach wall. The pancreas is represented by a small mass of tissue lying in the concavity of the proximal curve of the S-shaped duodenal tube. The body and tail of the gland are absent, and although no opening of a pancreatic duct is visible, a fine thread of tissue is observed attaching the mass to the duodenal wall.

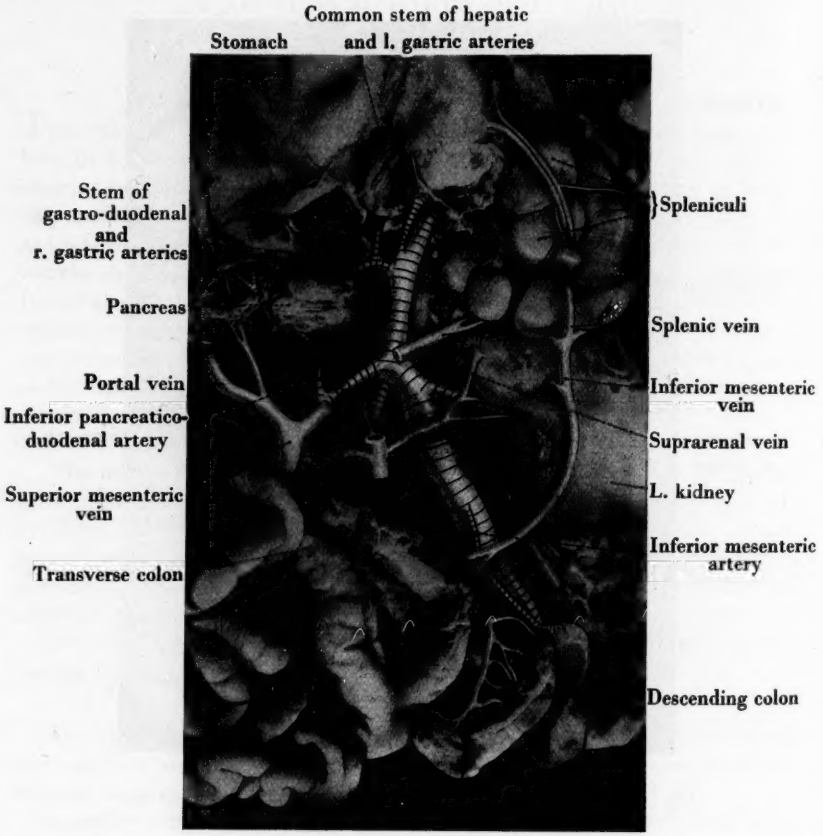

Fig. 2. View of further dissection of specimen showing vascular anomalies. As a result of the fixation of the specimen the abdominal aorta has become somewhat distorted.

Vascular abnormalities

The hepatic and left gastric arteries arise from the coeliac axis by a common stem. The former passes upwards to the left extremity of the transverse fissure of the liver, without giving off a gastro-duodenal branch. This latter

vessel arises directly from the coeliac axis by a stem common to it and the right gastric artery, and, passing behind the first part of the duodenum, forms the upper part of a vascular ring which surrounds the island of pancreatic tissue already referred to. The ring is completed distally by a branch (the inferior pancreatico-duodenal) from the superior mesenteric artery (fig. 2).

The portal vein, on the other hand, runs upwards *in front of* the first loop of the duodenum, and, accompanied by the common bile duct, enters the right extremity of the portal fissure, being separated from the hepatic artery by a large nodule of the liver which apparently represents the caudate lobe.

The most remarkable vascular anomaly, however, is found in the blood supply of the spleen. The splenic artery is absent, while the inferior mesenteric vein is found running upwards to the splenic region where it divides into numerous branches which enter the spleniculi. A separate branch of the vein runs to the left extremity of the greater curvature of the stomach. From this point, and from the cluster of spleniculi, other veins emerge and unite to form a single vein which, running transversely, joins the superior mesenteric vein and forms the portal trunk.

The coeliac axis gives rise to a left suprarenal artery and a left phrenic artery.

COMMENTARY

One is naturally inclined to speculate concerning the causes which may have operated to produce the anomalies found in this specimen.

The position of the portal vein may be accounted for by a failure in development of the dorsal loop of communication between the right and left vitelline veins. In this case, apparently, only the left vitelline vein persisted. A similar abnormality was reported by H. O. Knight in 1921.

The small size of the pancreas may be explained if one can assume that only the ventral bud of the organ is present, the absence of the body and tail suggesting a failure to develop on the part of the dorsal bud. In this connection it is interesting to note the coincident absence of the splenic artery normally associated with the body and tail of the gland. In this specimen the diminutive gland is supplied by the anastomotic ring contributed to by the gastro-duodenal and superior mesenteric vessels. The vascular supply of the spleen through the inferior mesenteric vein is presumably a secondary arrangement compensatory to the failure of its normal source. In any case, if we may assume some original failure in such developmental processes as normally take place in the dorsal mesentery of the stomach and duodenum, we have a clue to the association of these four anomalies, viz.: (1) the absence of the larger part of the pancreas, (2) the position of the portal vein in front of the duodenum, (3) the absence of a splenic artery, and (4) the aberrant form of the spleen itself.

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PERSISTENT THYROGLOSSAL DUCT IN A RABBIT

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In the course of dissection of the neck of an adult female rabbit for the purpose of examining any structural changes which may have occurred in the thyroid after splenectomy, a very fine cord-like structure was found connected with the left lobe of the thyroid gland running for about a centimetre and a half in front of the cricoid and thyroid cartilages behind the hyoid bone. The whole thyroid gland with the cord-like structure attached to it was removed and sections were cut in series and stained with haematoxylin and eosin.

Under the microscope, the section of the cord-like structure revealed an irregular lumen, lined by columnar epithelium. The convolutions of the lining epithelium have produced gland-like depressions and enclosed areas which look like vesicles. The outermost coat was composed of fibrous tissue, and the intermediate one exhibited both fibrous and unstriped muscular tissue (fig. 1).

As the cord approached the thyroid gland the lumen became smaller and smaller and the vesicles in the internal coat increased in number and the external coat with the unstriated muscle fibres was found to be thinner too. None of these vesicles contained colloid material. Some accessory or aberrant thyroid bodies (as first described by Zuckerkandl in 1879) were found in the course of the duct in the neighbourhood of the left lateral lobe of the thyroid. Each aberrant mass with a thin connective tissue capsule consisted of vesicles lined by short columnar and cubical epithelium, without colloid, which are quite different from those of the adjoining thyroid gland (fig. 2). Fig. 3 shows the histological structure of one such aberrant mass, under a higher magnification.

The structure of the thyroid gland in the vicinity showed the presence of stored-up colloid material in the vesicles (by Hewers' method (3) of differential staining by (*a*) haematoxylin and congo-red and (*b*) methyl blue and orange G).

Since the finding of this cord-like structure the neck region of about twenty other experimental animals was dissected with the utmost care, but the same structure was found in none of them.

DISCUSSION

The thyroid is originally developed as a tubular duct which bifurcates and subsequently divides into a series of cellular cords from which the isthmus and the lateral lobes of the thyroid gland are developed. The presence of a cord in this situation connected with the thyroid gland, its internal coat lined by

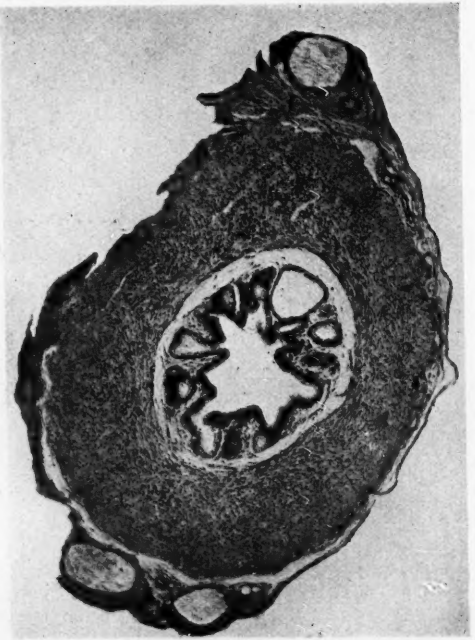

Fig. 1. Thyroglossal duct (under low power).

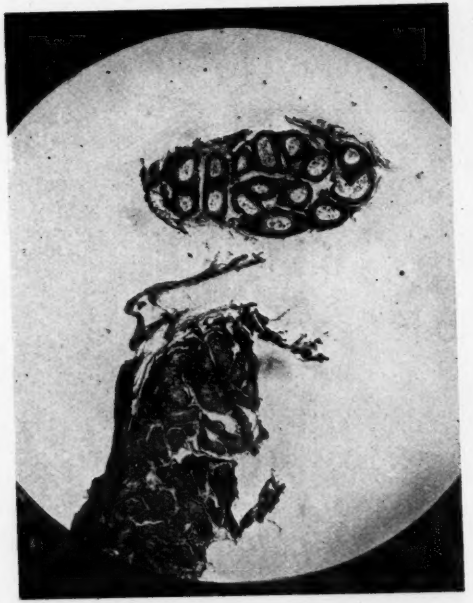

Fig. 2. Part of a thyroid lobe and an aberrant thyroid mass to show the difference in structure.

columnar epithelium with presence of vesicles as enclosures within its convolutions and external fibrous coat containing unstriped muscular fibres, all

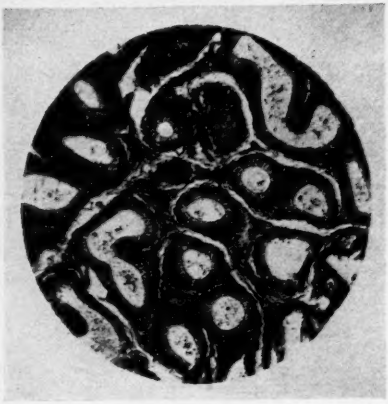

Fig. 3. Structure of an aberrant thyroid mass (in the neighbourhood of the duct).

suggest that the structure was a persistent thyroglossal duct. The presence of thyroid-like glandular masses in the course of the duct adds to the probability (4).

SUMMARY

The structure of a persistent thyroglossal duct in a rabbit is described. The most interesting feature of the observation is the continued differentiation of the thyroglossal duct until it resembles the alimentary tract with convoluted epithelium, tubular glands in the submucosa, internal and external muscular coats and the most external fibrous tunic.

I wish to express my thanks to Mr Hyder Ali Khan, F.R.C.S.E., Professor of Anatomy, Medical College, Patna, for kindly taking the micro-photographs, and Mr H. Banerji, of the department of Physiology, for assisting me in staining the sections.

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A CASE OF DISPLACED AND MALFORMED KIDNEY

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and S. C. SINHA, M.B., B.Sc.
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Congenital anomalies of the kidney are comparatively rare. In the Calcutta Medical College a very large number of post-mortem examinations and anatomical dissections are carried out annually, but during a period of nearly twenty years one case only of pelvic kidney, described by Prof. Pan (1) in 1924, has been observed. The following rare and interesting case is deemed worthy of record.

A Hindu male, aged 55 years, suffering from bilateral pulmonary tuberculosis, was admitted to the hospital in a moribund condition and died twenty-four hours later. At the necropsy a peculiar retro-peritoneal swelling which proved to be an abnormally placed left kidney was found lying opposite to the left sacro-iliac synchondrosis. The right kidney, with the exception of an abnormal arterial supply, was normal in position, size and shape and was provided with a normal hilum.

The left kidney (fig. 1), which was of average size, was lying obliquely upon the left iliac vessels; the upper pole was pointed and extended into the left iliac fossa, lateral to the 5th lumbar vertebra; the lower end, broader and more rounded, was lying along the adjacent part of the pelvic wall. The anterior surface was mainly occupied by a nearly vertical groove $3 \times \frac{1}{2}$ in., which obviously represented the hilum, as lodged in it were blood vessels, lymphatics, a few lymphnodes, nerves and the commencement of the ureter, together forming the pedicle of the kidney. The upper two-thirds of the groove was shallow and contained a renal artery with a companion vein and a duct, the latter being an elongated primary calyx. The lower third of the groove was deep and contained a sac formed by the junction of six ducts from different parts of the kidney. The sac was continuous with the ureter and represented a ureteric pelvis. The posterior surface was slightly concave and presented an oblique sulcus corresponding to the large iliac vessels on which the kidney was lying. The medial border was convex, gradually became thicker towards the lower pole, and probably represented the lateral border of a normal kidney. The lateral border was almost vertical, and at the junction of its lower and middle thirds was interrupted by a deep fissure which was occupied by a renal artery derived from the left common iliac artery.

The arterial supply of the left kidney (figs. 1 and 2) was derived from three sources. The largest and longest renal artery was a branch of the abdominal

aorta, given off half an inch below the origin of the inferior mesenteric artery. Before reaching the kidney it gave off a branch of moderate size, which was disposed on the upper part of the posterior renal surface. The main vessel coursed downwards on the medial side of the hilum, and after giving off numerous small branches finally ended by passing into the substance of the lower part of the kidney. The second artery was derived from the left common

Fig. 1. Anterior view.

iliac artery, half an inch above its bifurcation. It ran across the lower part of the posterior surface and curving round the lateral border in the fissure above mentioned (Fig. 2) thus gained the hilum. The third artery was a branch of the left hypogastric, and after a short course entered into the substance of the kidney on the posterior aspect of the lower pole (fig. 2).

Three left renal veins accompanied the three arteries and drained into the corresponding large vessels.

The left adrenal was normal in shape and size, and occupied the normal position.

In addition to a right renal artery, which exhibited little variation from the normal, the right kidney was provided with an aberrant artery derived from the aorta about 1 in. below the origin of the inferior mesenteric artery. This vessel passed obliquely upwards and laterally and crossed in front of the

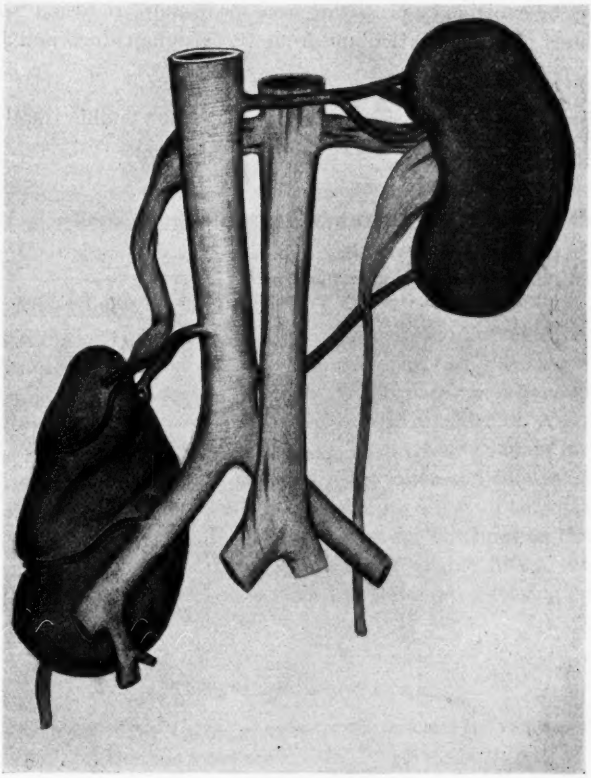

Fig. 2. Posterior view.

ureter to enter into the lower pole of the kidney. Above the point of crossing by this aberrant artery, the right ureter exhibited a dilatation which merged imperceptibly with the lower part of the pelvis. Behind the aberrant artery the ureter was narrow and constricted, a condition obviously caused by the pressure of the vessel (fig. 1). Otherwise the right ureter and its pelvis were normal.

Comments. The abnormalities of the left kidney here described may be

explained by a failure of the development changes which affect the kidney and account for its adult position and form. The normal relative displacement headwards has partially failed and the kidney occupied what may be regarded as an early foetal position; with this position the abnormal blood supply is associated. The rotation which the kidney normally undergoes has also failed; this accounts for the anterior position of the hilum and the medial position of the convex border. Further, the incomplete hilum and the exposure of the calyces may be explained as resulting from an incomplete fusion between the terminal buds of the diverticulum from the Wolffian duct and the metanephros.

We wish to express our sincere thanks to Master Sudhir Bhattacharyya, a second year student of this College, for his pencil sketches.

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CONCERNING THE COURSE OF THE LATERO-SENSORY CANALS IN RECENT FISHES, PRE-FISHES AND *NECTURUS*

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In connection with work I have under way it seemed desirable to establish, in so far as the literature at my disposal would permit, the homologies of the latero-sensory lines on the cheeks of Fishes. It, however, soon became apparent that their homologies could not be definitely established until their development was much better known than it is at present. Certain tentative conclusions regarding their homologies and also those of certain parts of the other sensory lines were, however, arrived at, and they seemed sufficiently important to warrant publication.

The descriptions of the sensory lines in a certain number of recent Fishes, and also those in *Necturus* and the Petromyzontidae, will therefore here be first reviewed as briefly as the purposes of this paper permit, and the canals in certain fossil Fishes and prefishes will then be considered. Nearly all of the figures given in illustration are purely diagrammatic, the main lines or canals alone being given without the related organs, pores and tubules. When a line or canal anastomoses in the median line with its fellow of the opposite side it is shown in contact with the outline of the figure. The lines on the dorsal and ventral surfaces of the head are shown as if visible in lateral view. The distinctive shadings of the several lines and the index-lettering employed are explained on page 415.

PETROMYZONTIDAE

The snout of these Cyclostomata is of viscero-trabeculo-cranial origin (Allis, 1932*a*) and there is no spiracle.

The main-infraorbital latero-sensory line in the Ammocoetes of *Petromyzon planeri* is said by Alcock (1898) to be a straight and nearly horizontal line which forms a direct anterior prolongation of the lateral line of the trunk. It lies between the dorsal and ventral divisions of the musculus capitis lateralis, and running forward first crosses the external surface of the otic capsule and then passes superficial to the eye which still lies deep beneath the external surface, and beyond that continues onward toward the end of the snout. In later stages of development, as the eye pushes its way outward toward the external surface, that part of the main-infraorbital line that in earlier stages lay directly superficial to it shifts ventrally and ultimately acquires a suborbital

position, the parts of the line that lie posterior and anterior to the eye retaining approximately their primitive positions. The suborbital portion of the line, as thus described by Alcock, now appears to form a somewhat detached and independent portion of the entire line, and I thus find it in small adults of *Entosphenus tridentatus* (fig. 1). There is accordingly in these specimens no part of the main-infraorbital line that has the topographical position of the postorbital section of the infraorbital canal of the gnathostome Fishes. In *Petromyzon dorsatus*, however, the anterior end of that part of the line that lies posterior to the eye is shown by Johnston (1905) bending downward behind the eye and so acquiring a postorbital position. In *Petromyzon planeri* and *Entosphenus tridentatus* the suborbital and antorbital portions of the line are both innervated by branches of the ramus buccalis lateralis (Allis, 1931 *b*) and the postorbital portion by branches of what Johnston calls the ramus communicans VII–X (VII–X anastomosis), the proximal portion of this nerve

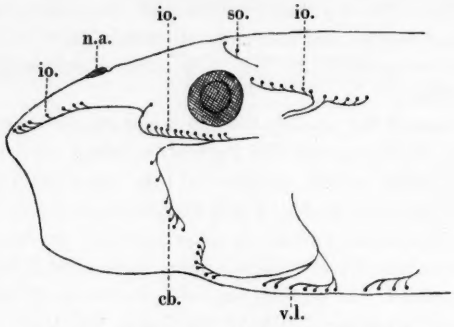

Fig. 1. *Entosphenus tridentatus*. Young adult.

being considered by him to correspond to the ramus oticus of the gnathostome Fishes.

The supraorbital line in both *Petromyzon planeri* and *Entosphenus tridentatus* is represented by one or two organs that lie on the dorsal surface of the head posterior to the single median nasal aperture and are innervated by the ramus ophthalmicus superficialis lateralis. Johnston, however, considers what corresponds in *Petromyzon dorsatus* to the anterior portion of the main-infraorbital of *Petromyzon planeri* and *Entosphenus tridentatus* to form an anterior division of the supraorbital and to be innervated by branches of the ramus ophthalmicus profundus, but this would seem to be incorrect, for the line lies lateral and hence morphologically ventral to the nasal capsule. No supratemporal line is described by either Alcock or Johnston, and I did not find it in *Entosphenus tridentatus*.

According to both Alcock and Johnston there is, in the specimens examined by them, a ventral line of pit organs which begins at the ventral edge of the buccal opening and from there extends posteriorly to the hind end of the

branchial basket. The prebranchial portion of this line is said by both authors to be innervated by a branch of the ramus hyomandibularis facialis, but they differ as to the innervation of the branchial portion. According to Alcock there is a latero-sensory nerve descending in each of the branchial arches and innervating the related portion of the ventral line, while according to Johnston such a nerve descends in the glossopharyngeus arch to innervate the related portion of the ventral line, the more posterior portion of the latter line being innervated by a nerve that runs downward posterior to the branchial basket and then forward ventral to it.

Alcock says that there is in the diaphragm of each branchial arch of *Petromyzon planeri* a number of sense organs that are innervated by a branch of the lateralis nerve that she finds running downward in each of these arches. Johnston says that in *Petromyzon dorsatus* these organs have the size, shape and general appearance of neuromasts, but that the sense cells are not furnished with terminal hairs. They are said by him to be innervated by communis fibres, and he accordingly considers them to be taste organs notwithstanding that they differ so markedly in size and shape from ordinary terminal buds.

No line corresponding to the preoperculo-mandibular line of Fishes is described either by Alcock or Johnston in *Petromyzon*, and I did not find it in *Entosphenus tridentatus*. I, however, found in the latter cyclostome a line of these organs, not described by either Alcock or Johnston, that begins slightly ventral to the anterior end of the suborbital section of the main-infraorbital line and from there extends ventrally and slightly posteriorly and nearly reaches the anterior end of the ventral line. A similar line is described by Razzauti (1916) in *Petromyzon planeri* as the circumbuccal line, and I found it innervated in *Entosphenus* by what is actually a branch of the ramus buccalis. This line would thus seem both in innervation and general position to belong to the mandibular arch, this suggesting that it may be the serial homologue in that arch of the so-called hyomandibular line of Platt's descriptions of early embryos of *Necturus*, to be considered immediately below.

NECTURUS

In early embryos of *Necturus* three longitudinal lines of thickened ectoderm are said by Platt (1896) to develop on each side of the head. These lines give rise to ridges which she calls the dorso-lateral, epibranchial and ventral, the epibranchial ridge lying between the other two along the dorsal edges of the gill clefts. Later, a series of transverse so-called intersegmental ridges develop, each ridge extending primarily from the dorso-lateral to the ventral longitudinal ridge. Dorsal to the epibranchial ridge these intersegmental ridges are said to lie between successive somites, and two of these somites are said to lie dorsal to the hyomandibular cleft. Ventral to the epibranchial ridge, the intersegmental ridges lie superficial to interbranchial expansions of the gut that later acquire contact with the internal surfaces of the overlying intersegmental ridges. The branchial clefts then break through along these

lines of contact and the related intersegmental ridges are broken down and dispersed, no latero-sensory organs developing in relation to them. The hyomandibular cleft does not break through, the related expansion of the gut losing its primarily acquired contact with the overlying intersegmental ridge and leaving the latter unbroken throughout its entire length. This ridge is called by Platt the hyomandibular, which because of the relation of the ridge to the hyomandibular cleft is eminently appropriate, but this same term, hyomandibular, is currently employed to designate, in the Elasmobranchii, certain totally different latero-sensory lines. The ventral end of the ridge anastomoses in *Necturus* with the ventral longitudinal ridge, and as the organs that later develop in relation to that part of the ventral ridge that lies anterior to this point of anastomosis are innervated by a nerve called by Platt the ramus hyomandibularis facialis, as are also the organs developed in relation to the so-called hyomandibular ridge, Platt includes both lines under the term hyomandibular. The so-formed line has the topographical position of the preoperculo-mandibular line of the Holostei and Teleostei, and also that of the spiracular-gular line of Garman's (1888) descriptions of *Chlamydoselachus*, which latter line I have considered to be the homologue of the preoperculo-mandibular line of the Holostei and Teleostei (Allis, 1928). There is, however, nothing in existing descriptions of *Chlamydoselachus* and the Holostei and Teleostei to indicate that the mandibular (gular) part of this line has been developed in relation to a pre-existing prebranchial portion of a ventral longitudinal line. Furthermore, the development of this line in *Ceratodus*, explained in the following section of this paper, would seem to establish that the ventral end of a line that corresponds to the so-called hyomandibular of early embryos of *Necturus* has simply swung forward and been prolonged into the mandible. There is thus question as to the exact homology of this line in these several Vertebrates, but it nevertheless seems best to call the line the preoperculo-mandibular, thus avoiding the use of the term hyomandibular.

From about the middle of the length of this preoperculo-mandibular (hyomandibular) line a so-called mandibular ridge is sent antero-ventrally into the mandible, where it comes into contact with the anterior end of the ventral longitudinal ridge. The dorsal end of the preoperculo-mandibular (hyomandibular) ridge later swings downward and forward and acquires contact with the postorbital section of the infraorbital ridge, the mandibular ridge at the same time losing contact with the preoperculo-mandibular (hyomandibular). The latero-sensory organs that later develop in relation to these two ridges, and also those that develop in relation to the prebranchial portion of the ventral longitudinal ridge, are all said to be innervated by branches of the ramus hyomandibularis facialis, as shown in the accompanying fig. 2 of a 19 mm. embryo. Two organs of the so-called mandibular line have become slightly detached and lie between its dorsal end and the adjacent portion of the infraorbital line. Like the other organs of the line they are innervated by branches of the ramus hyomandibularis facialis.

The primitive supraorbital ridge is said to be a direct anterior outgrowth of the primitive dorso-lateral longitudinal ridge, and the infraorbital to be a similar outgrowth of the epibranchial ridge. Two lines of latero-sensory organs develop in relation to the supraorbital ridge, the posterior halves of the two lines each being innervated by an independent branch of the ramus ophthalmicus lateralis, their anterior halves both being innervated by the lateral one alone of these two nerves. The line extends anteriorly beyond the external nasal aperture, and there, in the 19 mm. embryo, ends in a cluster of organs without indication of a recurrent course such as is found in most recent Fishes. The hind end of the mesial line turns dorso-posteriorly and suggests the anterior head line of pit organs of my descriptions of *Amia* (Allis, 1889).

The infraorbital line of the 19 mm. embryo runs downward behind the eye and then forward ventral to it and ends in a cluster of pores that lies between the eye and the external nasal aperture. It is innervated by the ramus

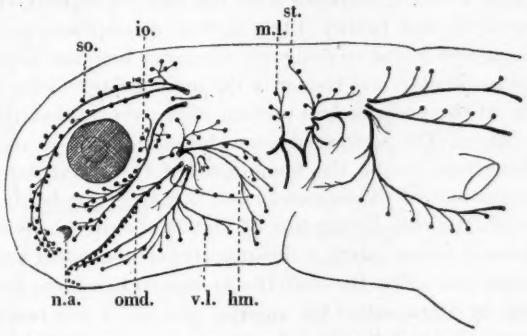

Fig. 2. *Necturus maculosis.* 19 mm. embryo. After Platt.

buccalis lateralis and is double throughout a part of its length. There are four organs shown in the figure lying immediately posterior to its postorbital section, and they are said to be innervated in this embryo by a branch of the buccalis. In other embryos organs that correspond topographically to these four are said to be innervated by a branch of the ramus hyomandibularis facialis, and Platt considers this to indicate that organs developed primarily in relation to the preoperculo-mandibular (hyomandibular) line have lost their innervation by the ramus hyomandibularis and acquired innervation by the ramus buccalis.

The single oticus organ, shown in the figure of the 19 mm. embryo, is said to have been developed in a sensory patch that was cut off from the dorso-posterior end of the infraorbital ridge in an earlier embryo, and it is innervated by a nerve, the ramus oticus, that has an independent origin from that part of the Gasserian ganglion that has been derived from the ectoderm. The rami buccalis and ophthalmicus superficialis also arise from this same part of the Gasserian ganglion, and when first segmented from the internal surfaces

of the supraorbital and infraorbital ridges they are considered to be trigeminus nerves, but when their roots later take what is said to be the shortest path to the brain and join the root of the nervus facialis they are considered to be branches of the latter nerve. In their terminal distribution these two nerves are, however, still strictly trigeminus nerves, but the relations of the ramus oticus to skeletal structures are apparently not definitely those of either a trigeminus or facialis nerve, and it might be considered to have belonged primarily to either of these two nerves.

There is, in the 19 mm. embryo, a group of sense organs that is innervated by the supratemporal branch of the nervus glossopharyngeus, and it apparently corresponds to the glossopharyngeus organ of the main-infraorbital line of *Amia* together with the middle head line of pit organs of that fish. Posterior to it there is a second group which is innervated by the supratemporal branch of the vagus, and corresponds to the vagus organs of the main-infraorbital line of *Amia* together with the posterior head line and the supratemporal line.

Kingsbury (1895) and Escher (1925) in their descriptions of the Amphibia employ the term postorbital to designate a sensory line that is the homologue of Platt's hyomandibular, and they give the name gular to what is apparently the homologue of the prebranchial portion of the ventral longitudinal line of Platt's descriptions. The so-formed postorbito-gular line is apparently considered by Kingsbury to be the homologue of the spiracular-gular line of Garman's descriptions of *Chlamydoselachus*, but this is probably incorrect, as above explained. The mandibular line of Platt's descriptions is considered by them to be formed of two parts, a dorso-posterior one called the jugular and a ventro-anterior one called the oral, the so-formed line being connected with the infraorbital by a line called the angular, this latter line being represented in Platt's descriptions of *Necturus* by the two organs that lie between the dorsal end of her mandibular line and the infraorbital. These three lines of the Amphibia correspond to the similarly named lines of Garman's descriptions of the Elasmobranchii, and they are usually called the hyomandibulars in recent descriptions of these Fishes.

DIPNOI

The nasal apertures of these Fishes lie on the ventral surface of the snout, and in the descriptions of embryos of *Ceratodus* there is nothing to indicate that the bucco-pharyngeal upper lip grows forward beyond the hind edges of the nasal pits. I accordingly concluded in an earlier work (Allis, 1932*a*) that the snout of these Fishes must be as it is in the Elasmobranchii of trabeculo-cranial origin. I, however, later called attention to the fact (Allis, 1932*b*) that, in *Ceratodus*, the hypophysis develops as a solid ingrowth of what corresponds to the deeper layer only of the two-layered ectoderm and not, as in the Elasmobranchii, in relation to a Rathke's pocket, and I now find that the latero-sensory canals of the adult *Ceratodus* are definitely of the teleostomian and not the elasmobranchian type. Furthermore, the primarily single nasal apertures of *Ceratodus* each later becomes subdivided into two by the develop-

ment of a typically teleostomian nasal bridge, instead of remaining incompletely separated into two as in the Elasmobranchii. There is therefore still question as to the character of the snout of these Fishes. There is no spiracle in the adult.

The latero-sensory canals of the adult *Ceratodus* were first described by v. Wijhe (1882) and later figured but not particularly described by Karl Fuerbringer (1904), and as given by the latter author they are reproduced in the accompanying fig. 3. The canals are said to be large, to lie wholly in the dermis superficial to the cranial bones and, according to Fuerbringer, they develop exactly in the manner described by me in *Amia*. The primary tubes are said by him to be small and subject to repeated dichotomous subdivision, certain of them being thus converted into large and delicately branching dendritic systems similar to those in *Amia*.

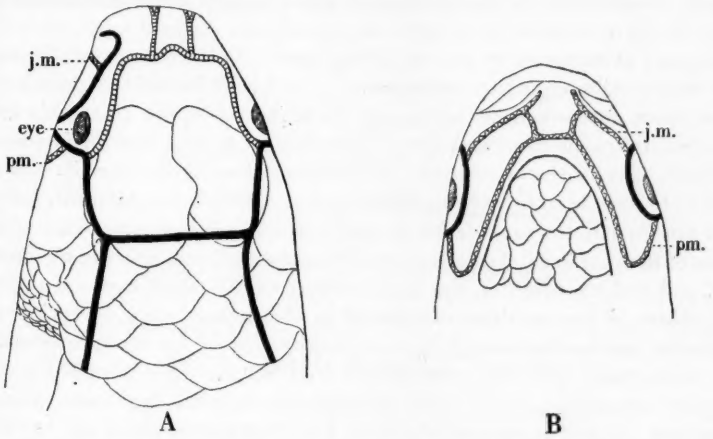

Fig. 3. *Ceratodus forsteri*. Dorso-lateral and ventral views of adult. After K. Fuerbringer.

The main-infraorbital canal running forward first anastomoses with the lateral end of the supratemporal canal and then continuing onward reaches the dorso-posterior border of the eye, where it anastomoses with the hind end of the supraorbital, this latter canal having been considered by v. Wijhe to form the direct anterior prolongation of the main canal. After this anastomosis, the main-infraorbital turns downward behind the eye and then forward ventral to it, beyond which it continues onward toward the end of the snout, where it turns laterally then postero-ventrally and ends without connection either with its fellow of the opposite side or with the supraorbital canal. This hook-like bend of the canal lies dorso-mesial to the nasal apertures of its side of the head and hence morphologically dorsal to the nasal capsule, this suggesting a part of the supranasal loop of this canal in *Raia* to be described below. The canal is said by v. Wijhe to be innervated from the point where it

anastomoses with the lateral end of the supratemporal canal forward to its anterior end by branches of the rami oticus and buccalis lateralis, the part innervated by the ramus oticus being said to extend anteriorly somewhat beyond the point of anastomosis with the hind end of the supraorbital. This is, however, not in accord with Greil's descriptions of the innervation in embryos given immediately below.

The supratemporal canal runs dorso-mesially and meets and anastomoses in the median line with its fellow of the opposite side. It is said to be innervated by the supratemporal branch of the nervus vagus.

The supraorbital canal anastomoses by its hind end with the main-infraorbital between its horizontal and postorbital sections and from there runs forward dorsal to the eye until, as shown in Fuerbringer's figure, it reaches a point about half-way between the eye and the tip of the snout, where it lies slightly mesial to the infraorbital canal not far from its hook-like anterior end. There it turns mesially at a right angle and then forward again at a right angle, and so continues to the end of the snout. At the point where it makes this second right angle turn it is connected with its fellow of the opposite side by a short cross-commissural canal. V. Wijhe could not trace this cross-commissural connection, and there is question as to just how far forward he was able to trace the canal itself. As far forward as he did trace it, it is said by him to have been innervated by the ramus ophthalmicus lateralis, but this does not include the innervation of the cross-commissural canal. An anastomosis of the supraorbital canals of opposite sides with each other in the median line, and so far forward on the dorsal surface of the snout, does not occur in any others of the craniates considered in the present work excepting only *Chimaera*, but a cross-commissural connection formed by the anastomosis of the supraorbital with the ethmoidal section of the main-infraorbital is of frequent occurrence, and it may be that this is what has taken place in *Ceratodus*. In the accompanying figure the commissural canal and the short branch that runs forward from it to the end of the snout are, however, shaded as if they formed part of the supraorbital canal. This will be further considered when describing the conditions in embryos, immediately below.

At the postero-ventral border of the eye the main-infraorbital canal gives off a branch which v. Wijhe calls the mandibular, this branch first running postero-ventrally on the cheek and then turning ventro-antero-mesially on to the mandible, where it is said to meet in the median line and run directly into its fellow of the opposite side. Slightly anterior to the eye a second so-called mandibular branch is given off from the main-infraorbital, this branch running downward into the mandible and then forward near the dorsal edge of the lower lip, and it is said by v. Wijhe to there meet and fuse in the median line with its fellow of the opposite side. Fuerbringer, however, shows this canal ending before it reaches the median line, but near its anterior end a branch is sent posteriorly to meet and anastomose with the posterior mandibular canal of v. Wijhe's descriptions. The latter canal is said by v. Wijhe to be innervated

by the ramus mandibularis externus facialis, but he does not give the innervation of the anterior mandibular canal.

In embryos of this fish the general arrangement of the latero-sensory lines, as described by Greil (1913), differs markedly in certain respects from that of the canals in the adult. He gives a diagrammatic figure purporting to show the sensory lines in an embryo of Stage 44, but gives no concise and connected description of the lines either in this embryo or in the older ones considered. The terms employed by him to designate the several canals are frequently changed and the innervation of certain parts of certain of them is nowhere definitely given.

In early embryos an ectodermal thickening is said to develop external to the dorsal end of what Greil calls the premandibular visceral pouch, but as this pouch lies between the mandibular and premandibular arches I shall refer to it as the mandibulo-premandibular. A second thickening is said to develop

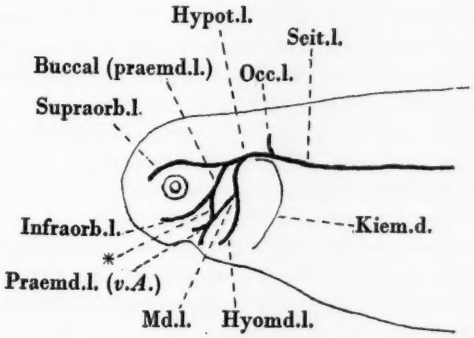

Fig. 4. *Ceratodus forsteri*. Embryo Stage 44. After Greil.

external to the dorsal end of the hyomandibular visceral pouch, this thickening and the anterior one later fusing to form what is called the preauditory thickening. From the anterior one of these two thickenings three sensory lines arise, a supraorbital, an hypoticus, also called the temporal, and a line that is said to run downward external to the outer edge of the mandibulo-premandibular visceral pouch. Greil gives to this latter line several names, calling it the premandibular, the buccal or the buccal (premandibular), but because of its relation to the mandibulo-premandibular pouch I shall call it the mandibulo-premandibular. These three sensory lines and the hyomandibular line are all said to grow outward from their centres of origin in a manner that is apparently strictly comparable to that in which the lateral line of the body grows progressively backward from its centre of origin (Greil, 1913, p. 963).

The mandibulo-premandibular line runs downward behind the eye and enters the mandible, there lying near the upper edge of the lower lip. Just

before entering the mandible it coalesces for a short distance with a so-called mandibular branch of the hyomandibular line described immediately below. Its dorsal portion is said to be innervated by the ramus buccalis, but the innervation of the ventral portion of the line is not definitely given. In one of the figures of transverse sections a branch of the ramus buccalis is, however, shown in the mandible not far from this sensory line, which would seem to indicate that the line was innervated by that nerve throughout its entire length. Slightly ventral to the eye, a branch is sent forward from the line in a suborbital position and is called both the infraorbital and the buccal. Its course is not described in detail and it cannot be definitely followed in the numerous figures of sections. In a figure (p. 1208) of a horizontal section through an embryo of Stage 46½, an organ of the line is shown lying lateral to the passage leading from the nasal sac to the apertures on the ventral surface of the snout, and continuous with it there is a line of surface organs directed mesially along what must be the dorsal surface of the tip of the snout and approaching but not actually meeting its fellow of the opposite side. These transversely placed organs are index-lettered as belonging to the infraorbital line, and the first organ in this embryo that is index-lettered as belonging to the supraorbital line is shown in a figure of a section that lies considerably dorsal to this one, and it is not connected with its fellow of the opposite side by a transverse line of organs. In a figure (p. 1437) of a horizontal section through an embryo of Stage 48, an organ index-lettered as belonging to the infraorbital line is shown lying lateral to the anterior nasal passage. Slightly anterior to it there is an organ index-lettered supraorbital, and continuous with it there is a transverse line that would seem to have exactly the position of the transverse so-called infraorbital line of the embryo of Stage 46½. This transverse line is, however, here index-lettered supraorbital, and a similar transverse line is shown in several figures of horizontal sections of the same embryo lying dorsal to this one. It therefore seems quite probable that there are here at least two transversely placed lines, but their innervation is not definitely given. The presence of two lines, however, strongly suggests the U-shaped ethmoidal canals of *Chlamydoselachus*, *Conger* and *Osteolepis*, to be later described, but the ethmoidal canals of these latter Fishes are innervated by branches of the ramus buccalis that pass latero-ventral to the nasal apertures and hence morphologically ventral to the nasal capsule, and no such branch of this nerve is shown by Greil in his figures of *Ceratodus*. The anterior portion of the ramus buccalis of *Protopterus* is, however, said by Pinkus (1895) to run forward ventral to the nasal capsule, as explained immediately below. There is therefore doubt as to the conditions in *Ceratodus*. If the anterior ends of the longitudinal portions of the infraorbital and supraorbital lines of these embryos, that is the anterior ends of those parts of these lines that lie posterior to the transverse commissures, were to fuse with each other, and the transverse commissures were to break down and be dispersed, the conditions shown in Fuerbringer's figure of the adult *Protopterus* would arise.

The supraorbital line of embryos of *Ceratodus* and the horizontal portion of the main-infraorbital do not differ topographically from those in the adult. That part of the main line that lies between its points of anastomosis with the supratemporal and supraorbital lines is called by Greil the hypoticus (hypotische), its preauditory portion being said to be innervated by the ramus hypoticus (oticus) and its postauditory portion by the supratemporal branch of the nervus glossopharyngeus, this not being in accord with v. Wijhe's descriptions of the innervation in the adult.

The dorsal end of the hyomandibular visceral pouch is said to retain its contact with the ectoderm after the remainder of the pouch has separated from it, and at this point of contact what Greil calls the hyomandibular Schlundtaschenorgan arises. It is said to be innervated by the ramus hypoticus (oticus), and as it lies at the dorsal end of a dorsal diverticulum of the hyomandibular visceral pouch it is evidently the homologue of the spiracular organs of *Amia* and *Lepidosteus*.

The so-called hyomandibular line of Greil's descriptions arises from the posterior portion of the preauditory ectodermal thickening and from there grows downward external to the outer edge of the hyomandibular visceral pouch, and it is said to be innervated throughout its entire length by what Greil calls the ramus hyomandibularis facialis. From it, somewhat ventral to its dorsal end, a so-called mandibular branch is said to arise and from there to grow antero-ventrally into the mandible, coalescing for a short distance and not far from its ventral end with the mandibulo-premandibular line, as above stated. This so-called mandibular line is evidently the homologue of the similarly named line of Platt's descriptions of *Necturus*, and for reasons to be given when considering the conditions in the Selachii I shall call it the jugal-oralomandibular. It is said to be innervated throughout its entire length by the ramus mandibularis externus facialis, this nerve being said to be a branch of the ramus hyomandibularis facialis.

A ventral longitudinal line, not shown in the diagrammatic figure, is said to begin immediately posterior to the hyal arch and from there extend posteriorly ventral to the branchial clefts. It is innervated by what is called a recurrent branch of the nervus vagus which runs downward behind the branchial arches and then forward ventral to them. The prehyal portion of this line found in *Necturus* is not described by Greil in embryos of *Ceratodus*, nor by v. Wijhe or Fuerbringer in the adult.

Comparing the conditions in embryos with those in the adult it is evident that certain parts of certain of the sensory lines of embryos have apparently wholly disappeared in the adult, while other parts have shifted considerably in position. There is nothing to indicate that any of the organs developed in relation to one of the lines have later acquired secondary innervation by the nerve of another line. The general course of the supraorbital and main-infraorbital lines of the adult is the same as that in embryos, but what is apparently an ethmoidal section of the main-infraorbital in embryos is either

wholly wanting in the adult, or has there fused with the anterior end of the supraorbital canal as it does in certain other Fishes. The main-infraorbital line is not throughout its entire length a direct forward prolongation of the lateral line of the body. It is in fact developed in what are apparently three independent sections, a horizontal epibranchial section which extends forward to the point of anastomosis with the hind end of the supraorbital, a descending mandibulo-premandibular section which has a postorbital position, and a suborbital section which develops in relation to an anteriorly directed branch of the mandibulo-premandibular line. The oticus section of the main-infraorbital line is thus not morphologically a part of the infraorbital portion of the main-infraorbital, and it seems probable that the ramus oticus which innervates this part of the horizontal line and also the spiracular organ which is said to develop definitely in relation to the hyomandibular sensory line is a facialis nerve and not, like the buccalis and ophthalmicus superficialis, a branch of the trigeminus. The dorsal end of the so-called hyomandibular line of embryos has swung forward and downward and acquired anastomosis with the postorbital section of the main-infraorbital, the ventral end of the line at the same time growing forward into the mandible, thus giving origin to the posterior mandibular canal of v. Wijhe's descriptions of the adult. This line is evidently the homologue of the spiracular-gular line of Garman's (1888) descriptions of *Chlamydoselachus* and also of the preoperculo-mandibular line of the Holostei and Teleostei, and there is nothing either in the figures or descriptions to indicate that a prebranchial portion of the ventral longitudinal line has taken any part in its formation. The ventral portion of the mandibulo-premandibular line of embryos of Stage 44 has become greatly reduced in embryos of Stage 48 and has apparently wholly disappeared in the adult. As it became reduced and withdrawn from the mandible, it dragged after it that part of the jugal-oralomandibular line to which it was attached by anastomosis, the dorsal end of the latter line at the same time shifting its point of attachment to the so-called hyomandibular (preoperculo-mandibular) line downward along that line. The jugal-oralomandibular line was thus bent at an angle, the point of the angle being directed toward the suborbital portion of the main-infraorbital and ultimately acquiring anastomosis with it. The preanastomosis portion of the jugal-oralomandibular then became the anterior mandibular canal of the adult, and the postanastomosis portion the short canal connecting the anterior mandibular canal of the adult with the posterior one.

In *Protopterus annectens* (fig. 5), as described and figured by Karl Fuerbringer (1904), the latero-sensory lines, as I interpret them, differ markedly from those in *Ceratodus*. The main-infraorbital line runs forward to a point considerably posterior and somewhat ventral to the eye and there anastomoses with what has the appearance of being the hind end of the supraorbital line, but at this point of anastomosis another sensory line begins and extending dorso-antero-mesially meets and anastomoses in the median line with its fellow of the opposite side. This latter line has thus the appearance of being a direct

posterior prolongation of the supraorbital line, and is evidently the homologue either of the anterior head line, alone, of pit organs of *Amia*, or of that head line together with the posterior portion of the supraorbital line. Posterior to this there are two branch lines sent dorso-mesially from the main-infraorbital, the posterior one of which meets and anastomoses in the median line with its fellow of the opposite side and would seem to be the supratemporal line, the other one probably being a middle head line.

After anastomosing with the supraorbital line the main-infraorbital runs antero-ventrally nearly to the angle of the gape, where it turns antero-dorsally ventral to the eye and then onward dorsal to the nasal capsule, anastomosing near the anterior end of the snout with the anterior end of the supraorbital

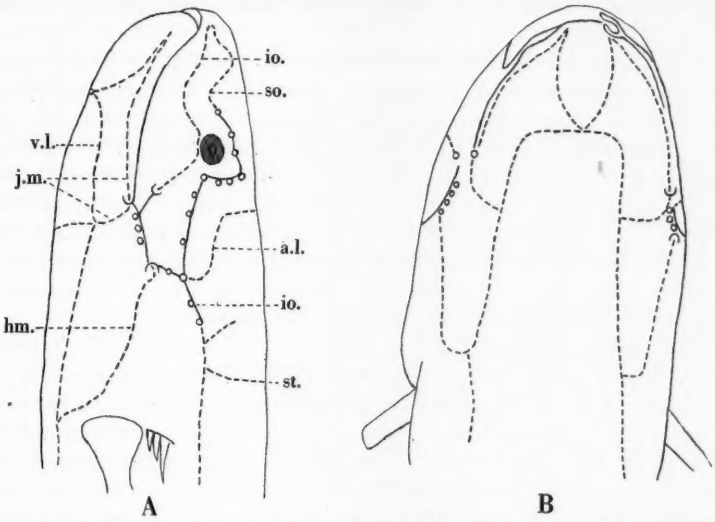

Fig. 5. *Protopterus annectens.* Lateral and ventral views of adult. After K. Fuerbringer.

line. In the specimen of this fish described by Pinkus and above referred to, these two lines do not here anastomose with each other, the infraorbital turning laterally and passing over the lateral edge of the snout anterior to a slight prominence that apparently represents the bulging dorsal surface of the nasal capsule, while the supraorbital turns mesially and, so far as can be judged from the figure, meets in the median line and anastomoses with its fellow of the opposite side. At about the middle of the length of the postorbital portion of the main-infraorbital a branch is shown by Fuerbringer running postero-ventrally in a slightly curved line and anastomosing distally with a ventral longitudinal line which extends from there forward into the lower jaw. This branch evidently corresponds to the hyomandibular line of Platt's descriptions of early embryos of *Necturus*, and taken together with that part of the ventral line that lies anterior to it corresponds to her descriptions of the

hyomandibular line of the 19 mm. embryo. This line is apparently the analogue but not the homologue of the so-called hyomandibular (preoperculo-mandibular) line of embryos of *Ceratodus*. At the angle between the postorbital and suborbital portions of the main-infraorbital a branch line is sent downward and forward in the lower jaw, there lying close to the dorsal edge of the lower lip, this line forming a direct prolongation of the postorbital portion of the main-infraorbital line and evidently corresponding to the anterior mandibular canal of v. Wijhe's descriptions of the adult *Ceratodus*. At the angle of the gape a branch canal arises from this anterior mandibular line and running ventrally and but slightly posteriorly anastomoses with the ventral longitudinal line, this short line apparently corresponding to the canal that in the adult *Ceratodus* connects the anterior and posterior mandibular canals of v. Wijhe's descriptions.

The supraorbital line may be considered to begin at the point where it anastomoses with the main-infraorbital. From there it extends forward until it reaches the ventro-posterior margin of the eye, where it turns upward in a strictly postorbital position and then forward above the eye, and so continues until it reaches the anterior end of the snout, where it anastomoses with the anterior end of the infraorbital line and there ends. This line and the suborbital portion of the infraorbital together have the appearance of forming a large supranasal loop similar to that in the Selachii, to be later described, but the course of these lines in the specimen described by Pinkus shows that the ventro-lateral limb of this loop belongs to the infraorbital.

The ventral longitudinal line in that part of its course that is shown in fig. 5 is nearly parallel to and somewhat widely separated from its fellow of the opposite side. Running forward, it first anastomoses with the ventral end of the so-called hyomandibular (preoperculo-mandibular) line and then with the short line that arises from the anterior mandibular line at the angle of the gape. Continuing onward beyond this for a certain distance it turns mesially at nearly a right angle, and after meeting in the median line and anastomosing with its fellow of the opposite side turns abruptly anteriorly and somewhat laterally and continuing in that direction toward the tip of the jaw closely approaches, but does not anastomose with, the anterior end of the anterior mandibular line. The anterior ends of the ventral lines of opposite sides thus together form a large median V, the point of which is directed posteriorly.

The innervation of these several lines cannot be definitely determined from Pinkus' descriptions. The ramus ophthalmicus superficialis, which is said to be a branch of the lateralis facialis, is said to send branches to the skin and numerous fine twigs to latero-sensory organs, especially those of the supraorbital line. The ramus buccalis is said to send branches to organs both of the supraorbital and infraorbital lines and other branches to the skin, the branches sent to the infraorbital line necessarily passing dorsal to the nasal capsule as the organs it innervates do. The main trunk of the buccalis is nevertheless said to run forward ventral to the nasal capsule, there being accompanied by a

branch of the ramus ophthalmicus profundus. There is no latero-sensory line shown either by Pinkus or Fuerbringer running forward ventral to the nasal capsule. If this part of the buccalis that is said to run forward ventral to the nasal capsule supplies latero-sensory organs it would seem as if they must form a detached ethmoidal line such as I have suggested might be present in *Ceratodus*. No branch of the buccalis is shown running downward into the lower jaw. A sensory organ is described in the dorsal wall of what is said to be a cubical vesicle enclosed in the cartilage of the cranium and it is said to be innervated by the ramus buccalis. A delicate canal runs inward from the vesicle, but ends blindly without reaching the pharyngeal cavity. This organ is evidently the homologue of the spiracular organ of *Ceratodus*, called by Greil the hyomandibular Schlundtaschenorgan, but in *Protopterus* the vesicle in the wall in which it lies has been entirely cut off from the pharyngeal cavity.

What may innervate what I have called the anterior mandibular line is not indicated.

SELACHII

In most of these Fishes and probably in all of them the snout is of trabeculo-cranial origin and the nasal apertures lie either on its ventral or ventro-lateral surfaces. A spiracle is said to be present in most of these Fishes, and in certain of them a spiracular diverticulum has been described, at the dorsal end of which there is a patch of sensory tissue innervated by the ramus oticus (Wright, 1885; Allis, 1901).

Chlamydoselachus anguineus (fig. 6) is considered to be a persistent type that closely resembles its ancestors of the Devonian age (Smith Woodward, 1921). The mouth is practically terminal, as it was in the Acanthodii and Chladoselachidae, and it is therefore probable that the latero-sensory canals present an archaic condition.

The main-infraorbital canal (Allis, 1923) is a direct anterior prolongation of the lateral line of the body, and after anastomosing with the lateral end of the supratemporal canal it continues onward to the dorso-posterior margin of the eye where it anastomoses with the hind end of the supraorbital. It then curves downward posterior to the eye and forward ventral to it, and near the anterior margin of the eye anastomoses with the morphologically anterior end of the supraorbital canal. It then continues onward ventro-mesial to the nasal apertures of its side of the head, and beyond them curves antero-mesially on the ventral surface of the tip of the snout and reaches the median line. There it makes a narrow U-shaped bend, and after extending latero-posteriorly a short distance turns dorso-postero-laterally and closely approaches (Allis) or actually anastomoses (Garman) with the supraorbital canal at the summit of the large supranasal loop of that canal. At the summit of the U-shaped bend it is in contact with its fellow of the opposite side, but whether the two canals here remain separated by a delicate membrane or are in complete anastomosis I could not tell from my dissections. It is, however, certain that the canals of opposite sides here form a cross-commissural ethmoidal canal which is

double throughout the larger part of its length, this offering an explanation of certain features of the ethmoidal canal of the Teleostomi that I have heretofore been unable to explain.

That part of the main-infraorbital that lies between its points of anastomosis with the supratemporal and supraorbital canals is innervated partly by the supratemporal branch of the nervus glossopharyngeus and partly by the ramus oticus lateralis, that part of the canal that lies anterior to its point of anastomosis with the supraorbital being innervated throughout its entire length by the ramus buccalis lateralis.

The supratemporal canal is short, lies actually anterior to the transverse line of the external opening of the endolymphatic ducts, but probably morphologically posterior to those openings (Allis, 1923 p. 76). It does not meet in

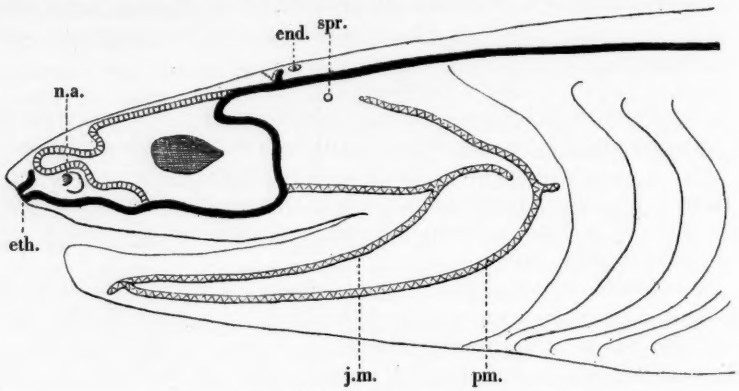

Fig. 6. *Chlamydoselachus anguineus*. After Allis.

the median line its fellow of the opposite side. It is innervated by the supratemporal branch of the nervus vagus and was double on one side of the head of the specimen examined. Immediately anterior to it there were one or two slight creases in the dermis which may have represented lines of surface organs, but they were not examined microscopically.

The supraorbital canal anastomoses by its hind end with the main-infraorbital between its horizontal and postorbital portions. From there it runs forward to the anterior end of the snout, where it curves laterally and then posteriorly and repassing dorso-mesial to the nasal apertures turns ventro-posteriorly between these apertures and the eye and falls into the main-infraorbital approximately at the anterior end of its suborbital section. The canal thus describes in its anterior portion a large loop which, as it lies dorsal to the nasal capsule, may be called the supranasal loop. The summit of this loop closely approaches if it does not actually anastomose with the anterior end of the main-infraorbital canal, as just above explained. The canal is innervated throughout its entire length by the ramus ophthalmicus lateralis.

On the cheek of the fish there are two latero-sensory lines lying somewhat concentric to each other. The posterior one of the two begins slightly posterior to the spiracle and from there runs first ventro-posteriorly and then ventro-anteriorly and entering the lower jaw extends nearly to its tip. It is evidently the homologue of the preoperculo-mandibular line of the Holostei and Teleostei, as I formerly considered it to be. The other one of the two lines has two parts which were called by Garman the angular-jugular and oral, and they correspond respectively to the hyomandibular and mandibular canals of current descriptions of others of the Selachii. The angular-jugular arises from the main-infraorbital between its postorbital and suborbital portions and from there runs posteriorly across the cheek. The oral arises from it at about its posterior third and from there runs antero-ventrally into the mandible, there anastomosing by its antero-ventral end with the preoperculo-mandibular line not far from its anterior end. Stensiö (1921) has given the name "jugal" to a canal in *Wimania* that is quite certainly the homologue of the angular-jugular line of *Chlamydoselachus*, and I shall adopt this term, the oral line being called the oralomandibular. The entire line will then become the jugal-oralomandibular, and it is to be noted that that part of this line that lies in the mandible cannot be the homologue of the mandibular part of the preoperculo-mandibular line, for both of these lines are present in this fish. The preoperculo-mandibular and jugal-oralomandibular are both innervated by branches of the ramus mandibularis externus facialis. Norris (1932) considers these two lines of *Chlamydoselachus* together to correspond to the so-called hyomandibular of Ewart and Mitchell's (1892) descriptions of *Raia*, that short portion of the spiracular-gular (preoperculo-mandibular) that lies anterior to its point of anastomosis with the oral (my oralomandibular) corresponding to the seventh division of the hyomandibular of *Raia* and hence to what is frequently called in descriptions of these Fishes the mandibular. This, however, seems to me incorrect.

In *Mustelus laevis*, as described by me (Allis, 1901) and shown in the accompanying fig. 7, the mouth is ventral and the nasal apertures lie anterior to it on the ventral surface of the snout.

The main-infraorbital canal running forward anastomoses first with the lateral end of the supratemporal canal and then with the hind end of the supraorbital. It then turns downward behind and forward ventral to the eye, but when it reaches the level of the anterior margin of the eye it curves ventrally, then ventro-posteriorly and finally anteriorly, thus here having an S-shaped course. At the summit of the ventral bend of the S it anastomoses with the anterior end of the jugal (so-called hyomandibular) canal, and at the anterior end of the ventral limb of the S it anastomoses with the morphologically anterior end of the supraorbital canal. That part of the main-infraorbital that lies between these two points of anastomosis thus corresponds, in so far as its relations to them are concerned, to the suborbital portion of the canal of *Chlamydoselachus*. The dorsal bend of the S, the summit of which

is directed anteriorly, thus corresponds to a part of the postorbital portion of the canal of *Chlamydoselachus* that has bulged forward below the eye, between it and the anterior end of the jugal canal. In *Raia*, this bulge of the canal becomes a large supranasal loop, as will be described below.

After the main-infraorbital has anastomosed with the anterior end of the supraorbital, as above described, it turns ventro-antero-mesially, and passing between the mouth-opening and the nasal apertures reaches the median line. There it turns forward between the apertures of opposite sides of the head and fuses for a short distance in the median line with its fellow of the opposite side to form what Garman calls the median canal, but which I shall refer to as the internasal anastomosis. Beyond this the main-infraorbital of either side runs anteriorly and slightly laterally on the ventral surface of the snout, and

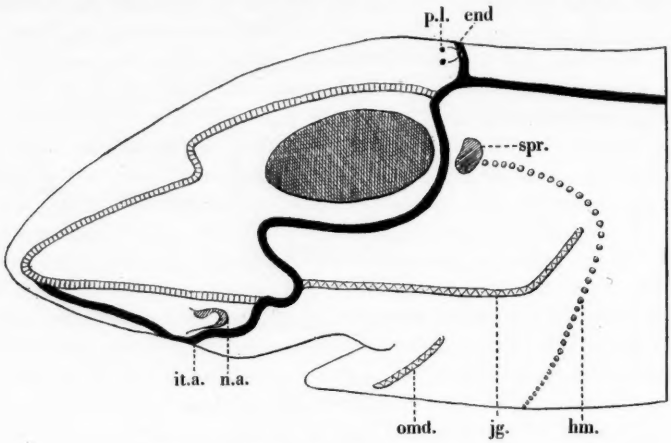

Fig. 7. *Mustelus laevis*. After Allis.

at its anterior end anastomoses with the supraorbital near the summit of the supranasal loop of the latter. The internasal anastomosis of the main-infraorbital canals of this fish must therefore correspond to what I have called in *Chlamydoselachus* the ethmoidal anastomosis, and the conditions in either one of these two Fishes could have been derived from that in the other in connection with the simple shifting backward or forward of the mouth-opening.

That part of the main-infraorbital of *Mustelus* that lies between its points of anastomosis with the supratemporal and supraorbital canals is innervated by the ramus oticus lateralis, the infraorbital part of the canal being innervated throughout its entire length by the ramus buccalis lateralis.

The supratemporal canal arises from the main-infraorbital immediately posterior to the section of the latter canal that is innervated by the ramus oticus and running dorso-mesially meets and anastomoses in the median line with its fellow of the opposite side. It lies approximately superficial to the

anterior end of the occipital portion of the chondrocranium and immediately posterior to the external opening of the endolymphatic duct of its side of the head. It is innervated by what was apparently a supratemporal branch of the nervus linae lateralis but which is probably the homologue of that supratemporal branch of the nervus vagus which in *Chlamydoselachus* innervates this canal. Immediately anterior to it there are two surface sense organs, one on either side of the external opening of the endolymphatic duct. I was unable to determine their innervation, but their position shows that they must correspond either to the middle or posterior head line of pit organs of *Amia*.

The jugal-oralomandibular line is entirely enclosed in a canal, but it presents two wholly independent portions which correspond the one to the jugal and the other to the oralomandibular parts of the line of *Chlamydoselachus*. The jugal canal arises from the main-infraorbital at the point shown in the figure, and from there extends posteriorly across the cheek. The oralomandibular line is short, lies apparently entirely in the mandible but extends dorso-posteriorly slightly beyond the angle of the gape of the mouth. Both it and the jugal are innervated by the ramus mandibularis externus facialis.

Posterior to the jugal-oralomandibular canal there is a line of surface organs which begins dorsally immediately posterior to the spiracle and from there extends at first ventro-posteriorly and then ventrally and but slightly anteriorly and reaches the ventral surface of the head, where it meets in the midventral line and is continuous with its fellow of the opposite side. I did not determine its innervation, but it is evidently the homologue of the so-called hyomandibular line of embryos of *Ceratodus*, and if its ventral end were to shift forward and be prolonged into the mandible it would quite certainly give origin to the spiracular-gular (preoperculo-mandibular) line of *Chlamydoselachus*, and it is quite certain that no part of a ventral longitudinal line has taken part in its formation.

In *Laemargus*, as described by Ewart (1892), the anterior end of the horizontal portion of the main-infraorbital canal turns mesially on the dorsal surface of the head and approaches but does not anastomose with the dorsal end of the postorbital section of the canal, the dorsal end of the latter canal anastomosing with the hind end of the supraorbital. This horizontal portion of the main-infraorbital is said to be innervated partly by the ramus oticus and partly by the supratemporal branch of the nervus vagus. The innervation of this section of the main-infraorbital is thus different in each of the three Selachii here under consideration, but what the cause or significance of this may be is not apparent. The jugal canal, called by Ewart the hyomandibular, arises from the main-infraorbital at approximately the angle between its postorbital and suborbital sections, and from there extends posteriorly across the cheek. The oralomandibular, called by Ewart the mandibular, arises from the jugal not far from its anterior end and from there runs downward into the mandible, both it and the jugal canal being innervated by branches of the

ramus mandibularis externus facialis. There is no indication in Ewart's descriptions of a preoperculo-mandibular latero-sensory line.

In a 29 mm. specimen of *Spinax niger*, Ruud (1920) shows the main-infraorbital line having the general course it has in the adult *Mustelus*, but ending at the anterior end of the snout without anastomosing with the supraorbital. The latter line is shown separated into so-called dorsal and ventral sections. The dorsal section anastomoses by its hind end with the main-infraorbital between its horizontal and postorbital portions and from there runs forward dorso-mesial to the eye and the nasal apertures until it reaches the anterior end of the snout. There it turns over that edge and reaches the ventral surface of the snout where it turns latero-posteriorly in a direction which, if prolonged, would pass dorso-mesial to the nasal apertures and there ends. The dorsal division of this canal therefore corresponds to the mesial limb of the supranasal loop of the canal in *Chlamydoselachus* and *Mustelus* together with a short anterior portion of the lateral limb of that loop. The other section of the line, called by Ruud the ventral, is said to have been segmented off from the recurrent end of the dorsal section. It begins at a certain distance posterior to that end of the dorsal section and from there runs postero-ventro-mesially between the nasal apertures and the eye, but does not reach and fall into the main-infraorbital line. In older embryos it does reach and anastomose with the main-infraorbital, but in the oldest embryos figured by Ruud it is still shown independent of the dorsal section. Brohmer (1908) shows this section of this line even in these early embryos turning postero-dorsally and anastomosing with the dorsal section dorso-mesial to the eye. This differs so much from Ruud's descriptions that it may not be correct, and it is here so particularly referred to simply because there is in the same place in certain teleosts an independent line of surface organs. In these embryos of *Spinax* the internasal anastomosis of the infraorbital lines has not yet taken place.

In a 23 mm. embryo of *Spinax niger*, Ruud shows what she calls a hyo-mandibular line of pit organs (Spaltpapillen) lying slightly anterior to and parallel to the hyobranchial cleft. Near its dorsal end there is a short branch projecting anteriorly which is evidently the homologue of the so-called mandibular line of Platt's and Greil's descriptions, respectively, of *Necturus* and *Ceratodus*. In the 29 mm. embryo the so-called hyomandibular line of surface organs has been prolonged dorsally nearly to the spiracle and ventrally on to the ventral surface of the head, thus corresponding definitely to the preoperculo-mandibular line of surface organs of my descriptions of the adult *Mustelus*. The small branch line directed anteriorly from it in the 23 mm. embryo has become detached and extends anteriorly across the cheek, ultimately reaching and anastomosing with the infraorbital line. This line is called by Ruud the hyomandibular and corresponds exactly to what I have called the jugal canal in the adult *Mustelus*, a line corresponding to the oralomandibular of my descriptions of *Mustelus* being said to be wholly wanting in *Spinax*.

BATOIDEI

In these Fishes the snout is of trabeculo-cranial origin, the nasal apertures lie on its ventral surface and a spiracle is usually if not always present. That part of the primitive bar of the hyal arch that lies ventral to the pharyngohyal becomes reduced or wholly suppressed in the adult and is replaced by a so-called pseudohyoideum developed from the branchial rays of the hyal arch, as fully described by Krivetsky (1917) and later confirmed by de Beer (1932). Associated with this the so-called hyomandibular canal has become greatly elongated and somewhat complicated in its course.

In *Raia batis*, as described by Ewart and Mitchell (1892), the main-infraorbital canal runs forward and after anastomosing with the supra-temporal and supraorbital canals turns downward behind and then forward ventral to the eye. Near the anterior margin of the latter and while still lying on the dorsal surface of the head it becomes connected by a group of tubules with a canal that lies actually lateral and hence morphologically ventral to it and is called by Ewart and Mitchell the hyomandibular. Beyond this the main-infraorbital continues onward nearly to the antero-lateral margin of the head, which it pierces and then turns postero-laterally on the ventral surface of the head and anastomoses first with the morphologically anterior end of the supraorbital and then with the anteriorly directed ventral end of the so-called hyomandibular. This latter anastomosis lies approximately in the same transverse plane as the anastomosis of these two canals on the dorsal surface of the head through the intermediation of tubules. The main-infra-orbital thus here describes a loop, the anteriorly directed limb of the loop lying actually lateral and hence morphologically ventral to that part of the supraorbital canal that lies on the dorsal surface of the head, the posteriorly directed limb lying actually lateral and hence morphologically dorsal to that part of the supraorbital canal that lies on the ventral surface of the head. This loop of the main-infraorbital is thus enclosed within a supranasal loop of the supraorbital canal that is strictly comparable to that above described in the Selachii, the loop of the infraorbital canal thus lying morphologically on the dorsal surface of the nasal capsule as shown in fig. 8, which gives in lateral view a projection of these canals on an outline of the head of *Mustelus*. At the point where the main-infraorbital anastomoses with the ventro-anterior end of the so-called hyomandibular, it turns sharply mesially posterior to the nasal apertures of its side of the head and then forward mesial to those apertures. There, as definitely shown by the innervation, it turns mesially and meets end to end in the median line and anastomoses with the corresponding part of its fellow of the opposite side, thus forming a transverse internasal commissure which replaces the side to side coalescence of these two canals in the Selachii. At the lateral end of this cross-commissure this part of the main-infraorbital canal anastomoses with the hind end of what Garman calls the prenasal portion of the entire canal which runs forward from there to the tip of the snout,

lying in this part of its course near the middle line of the head and close to and parallel to that portion of the supranasal loop of the supraorbital canal that lies on the ventral surface of the head. It is, however, to be particularly noted that although these two canals here lie close together and actually on the ventral surface of the head, their relations to the nasal apertures definitely show that the one lies morphologically ventral and the other dorsal to the nasal capsule. At the anterior end of the snout the main-infraorbital is said by Ewart and Mitchell to turn mesially and run directly into and be continuous with its fellow of the opposite side, but Garman does not show this anastomosis of these canals in any of the Batoidei described by him, which include *Raia laevis* and *Raia ocellata*. There is also in none of the Batoidei described by Garman an anastomosis of the anterior end of the main-infraorbital with

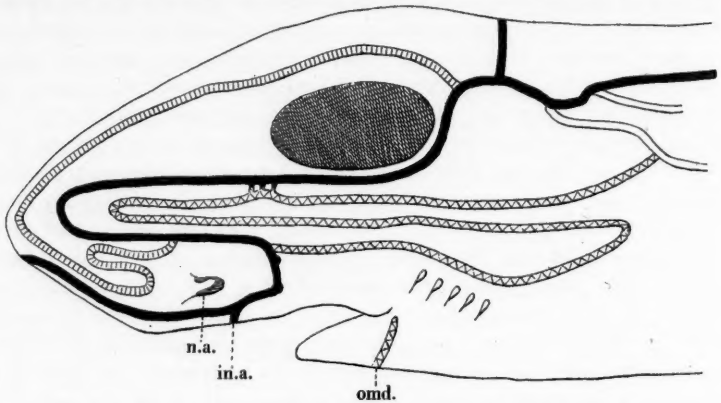

Fig. 8. Latero-sensory canals of *Raia batis*, after Ewart and Mitchell, projected on an outline of the head of *Mustelus laevis*.

the summit of the supranasal loop of the supraorbital such as is found in most of the Selachii.

That part of the main-infraorbital of *Raia* that lies between the points of anastomosis with the supratemporal and supraorbital canals is short and contains but two sense organs which are innervated by a branch of a nerve that apparently corresponds to the supratemporal branch of the nervus vagus of the Selachii above considered, the remainder of the canal being innervated by the ramus buccalis. There is accordingly no part of this canal of *Raia* innervated by a ramus oticus.

The supratemporal canal anastomoses in the median line with its fellow of the opposite side to form a complete cross-commissure and is innervated by the nerve above referred to that apparently corresponds to the supratemporal branch of the nervus vagus of the Selachii.

The supraorbital canal, starting from the point of anastomosis with the main-infraorbital between its horizontal and postorbital portions, runs forward

dorso-mesial both to the eye and the nasal apertures of its side of the head until it reaches the tip of the snout. There it pierces the snout and then runs postero-laterally on the ventral surface of the head in an irregular course until it meets and anastomoses with the main-infraorbital in the manner just above described, lying everywhere in this latter part of its course actually antero-lateral and hence morphologically dorsal to the nasal apertures. The anterior portion of the canal thus forms a large supranasal loop similar to that in the Selachii. The canal is said to be innervated throughout its entire length by the ramus ophthalmicus lateralis.

The so-called hyomandibular is a long and continuous canal that has in lateral view (fig. 8) the shape of a large and greatly flattened letter **S**. The dorsal bend of the **S** projects forward on to the dorsal surface of the nasal capsule, there forming a supranasal loop that lies within the supranasal loop of the main-infraorbital, the ventral bend of the **S** extending posteriorly dorsal to the gill clefts. The dorsal end of the **S** anastomoses with a canal that extends postero-latero-ventrally from the lateral canal of the body, the ventral end of the **S** anastomosing with the main-infraorbital as that canal turns antero-mesially to pass between the nasal apertures of opposite sides of the head. Between the two ends of this continuous canal there is still another connection with the main-infraorbital, but it is apparently formed by the fusion of primary tubules and not by direct anastomosis of the canals themselves. This canal is called by Ewart and Mitchell the hyomandibular 1, 2, 3, 4, 5, 6, and another canal called by them the hyomandibular 7 lies in a transverse position immediately posterior to the mouth and is continuous in the median line with its fellow of the opposite side. These two canals are innervated throughout their entire lengths by the ramus mandibularis externus facialis and are quite unquestionably the homologues, respectively, of what I have called in the Selachii the jugal and oralomandibular canals. There is nothing described in the text or shown in the figures that corresponds to what I have called in the Selachii the preoperculo-mandibular (hyomandibular) line. There may, however, have been surface sense organs representing this line and overlooked by the authors.

HOLOCEPHALI

In these Fishes the snout is quite certainly of the trabeculo-cranial type, as it is in the Plagiostomi, for the nasal apertures lie not only morphologically on its ventral surface but actually ventral to the trabeculae if I am correct in my contention that these latter cartilages form the roof of the forebrain cavity (Allis, 1926). The spiracle is said to be suppressed.

In *Chimaera monstrosa*, as described by Cole (1896), the latero-sensory lines are said to lie in open grooves instead of closed canals, and they have the general course shown in the accompanying fig. 9 which is a reproduction of the canals in my figure of *Chimaera colliei*. The supratemporal line is considered by Cole to be formed by the abrupt bending dorso-mesially of the anterior end of the lateral line of the body. Immediately anterior to it the main-infraorbital

line runs antero-ventrally to the postero-ventral margin of the orbit and throughout this part of its length the line is said by him to be innervated entirely by the ramus oticus lateralis. At the extreme anterior end of this oticus section of the line a branch line is sent antero-ventrally into the mandible, and slightly posterior to it and separated from it by a section of the main-infraorbital that lodges but a single oticus organ there is a second branch line which extends postero-ventrally across the cheek. Both of these lines are innervated by the ramus mandibularis externus facialis, are called by Cole the hyomandibulars and are evidently the homologues, respectively, of the oralomandibular and jugal lines just above described in the Plagiostomi. Anterior to the so-designated oralomandibular line the main-infraorbital is represented by two lines called by Cole, because of their innervation, the inner

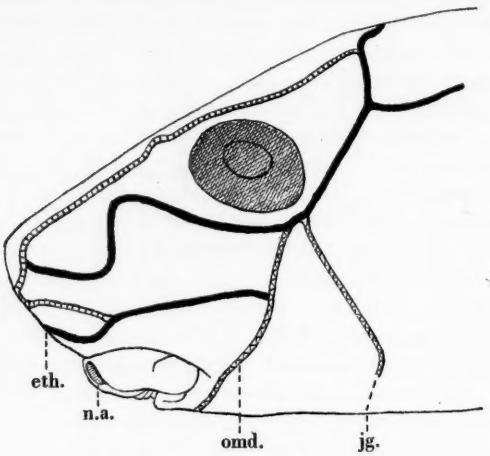

Fig. 9. *Chimaera colliei*. After Allis.

and outer buccals. The inner buccal is a direct anterior prolongation of the oticus section of the main-infraorbital, and running forward ventral to the eye takes an **S**-shaped course and anastomoses by its anterior end with the supraorbital line near the anterior end of the snout. The outer buccal line arises from the oralomandibular considerably dorso-posterior to the angle of the gape of the mouth, and running almost directly forward meets and anastomoses with the anterior end of the supraorbital line dorso-posterior to the external nasal apertures of its side of the head. Beyond that it continues onward dorsal to the nasal apertures and meets in the median line and runs directly into its fellow of the opposite side.

The supraorbital line anastomoses by its hind end with the supratemporal commissure instead of, as in the Plagiostomi, with the main-infraorbital. From there it runs almost directly forward dorsal to the eye until it reaches

the anterior end of the snout, where it turns ventrally and meets and anastomoses with the anterior end of the inner buccal line. It then continues ventro-mesially, meets and coalesces in the median line for a short distance with its fellow of the opposite side, and then turning postero-ventrally anastomoses by its anterior end with the outer buccal line as the latter line passes across the dorsal surface of the nasal capsule.

The conditions in *Chimaera* thus differ markedly from those in the other Elasmobranchii above considered, and this is quite certainly due to the shifting of the trabeculae from a position ventral to the forebrain cavity to one dorsal to that cavity and the correlated shifting of the eyeball, also, to a position dorsal to that cavity (Allis, 1917, 1926). This shifting of the eyeball has forced the posterior portion of the supraorbital line upward, and its hind end has acquired anastomosis with the supratemporal instead of with the main-infraorbital. The suborbital section of the main-infraorbital has followed the eyeball in this upward movement, but the antorbital section has apparently lagged behind retaining its customary position approximately superficial to the trabecula of its side of the head. It has accordingly lost its connection with the suborbital section and acquired a secondary connection with the oralo-mandibular line, and from there it runs forward dorsal to the nasal capsule.

There is no indication of a preoperculo-mandibular line.

CROSSOPTERYGII

In these Fishes the snout is quite certainly of viscero-trabeculo-cranial origin, for the nasal apertures lie definitely on its dorsal surface. The hypophysial canal, however, opens on the roof of the buccal cavity. It must therefore be that the primary opening of this canal was forced on to the dorsal surface of the snout by the forward growth of the bucco-pharyngeal upper lip, and that its actual attachment to the ectoderm has been secondarily acquired as it is known to be so acquired in *Acipenser* and probably also in the Teleostei (Allis, 1931 *a*; Holmgren, 1931). The spiracle persists, but I find no mention of a spiracular diverticulum with latero-sensory organs developed in relation to it.

In *Polypterus bichir* (fig. 10), as described by me (Allis, 1900, 1922), the main-infraorbital canal may be considered to begin at the hind edge of the posttemporal (suprascapular), this bone lodging the most posterior organ innervated by the supratemporal branch of the nervus vagus. From there the canal, running forward, anastomoses first with the lateral end of the supratemporal canal and then with the hind end of the supraorbital, the latter point of anastomosis lying a relatively considerable distance dorso-posterior to the external opening of the orbit, this being doubtless due to the fact that the eyeball occupies only the anterior half, approximately, of the long orbital fossa. From there the canal curves antero-ventrally behind the orbital opening and then forward ventral to both that opening and the external opening of the nasal pit, curving upward somewhat between these two openings. Anterior

to the nasal opening the canal turns mesially and passing on to the dorsal surface of the snout there meets in the median line and anastomoses with its fellow of the opposite side, thus forming the ethmoidal cross-commissural canal. Near the lateral end of this commissure there is a slight swelling in the dorso-posterior wall of the canal, and the canal there anastomoses with the summit of what may be called the supranasal hook of the supraorbital canal. Comparing the conditions in this fish with those in the Plagiostomi and more particularly with those in *Acipenser* and *Conger*, to be later described, it is evident that the ethmoidal canal of *Polypterus* is the homologue either of the simple internasal connection of the infraorbital canals of *Raia*, or has been formed by the coalescence of the two limbs of a U-shaped ethmoidal canal similar to that in *Chlamydoselachus*, and that in either case the slight swelling in the canal of *Polypterus* represents the morphologically anterior end of the infraorbital canal. Which of these two anastomoses has here taken place is uncertain, the single row of latero-sensory organs in the canal of *Polypterus*

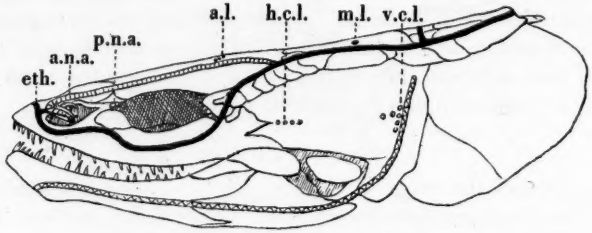

Fig. 10. *Polypterus bichir*. After Allis.

suggesting the anastomosis in *Raia*, while the conditions in *Conger* and in *Osteolepis* favour the U-shaped anastomosis of *Chlamydoselachus*.

That part of the main-infraorbital that lies between the points of anastomosis with the supratemporal and supraorbital canals lodges but two sense organs, the anterior one being innervated by the ramus oticus and the posterior one by the supratemporal branch of the nervus glossopharyngeus. The infraorbital part of the canal is innervated throughout its entire length by the ramus buccalis.

The supratemporal canal lies in the supratemporal (extrascapular) bones and meets and anastomoses in the middorsal line with its fellow of the opposite side. It is innervated by the supratemporal branch of the nervus vagus.

The supraorbital canal anastomoses by its hind end with the main-infraorbital between its horizontal and postorbital portions and from there runs forward dorso-mesial to the orbital and nasal openings until it reaches the anterior end of the snout. There it turns laterally and then postero-laterally and ends after traversing the os terminale which lies in the dermal roof of the nasal pit between the anterior and posterior nasal apertures. The canal thus here presents a hook-like appearance and corresponds to the dorso-

mesial section of the supranasal loop of Ruud's descriptions of early embryos of *Spinax niger*, excepting in that the anterior end of the hook passes between the two nasal apertures instead of, as in *Spinax*, dorso-mesial to a single incompletely subdivided aperture. At the summit of the hook the supraorbital anastomoses with the morphologically anterior end of the infraorbital canal, as just above explained. The canal is innervated throughout its entire length by the ramus ophthalmicus lateralis.

The preoperculo-mandibular canal begins immediately posterior to the large spiracular opening and from there runs downward and then forward into the mandible, where it meets and anastomoses in the median line with its fellow of the opposite side. It does not meet at its dorsal end and anastomose with the main-infraorbital. It is innervated throughout its entire length by the ramus mandibularis externus facialis.

On the dorsal surface of the head there are on either side two surface lines of pit organs which apparently correspond to the anterior and middle head lines of *Amia*. On the cheek there are horizontal and vertical cheek lines and on the ventral surface of the head a gular line, all of which correspond to the similarly named lines in *Amia*. The innervation of these several surface lines was not definitely determined excepting only that of the anterior head line which is innervated by a branch of the ramus ophthalmicus lateralis.

CHONDROSTEI

In *Acipenser*, and hence probably in all of the recent Chondrostei, the snout is of viscero-trabeculo-cranial origin, but the hypophysial canal has acquired secondary attachment to the external ectoderm on that part of the ventral surface of the snout that lies between the barbels and the mouth opening (Allis, 1931*a*; Holmgren, 1931). A spiracular opening is present in both *Polyodon* and *Acipenser*, but not in *Scaphirhynchus*. In *Polyodon* there is a spiracular diverticulum with a patch of sensory tissue at its dorsal end innervated by a branch of the ramus oticus, as will be fully explained in a later work, but this spiracular sense organ has not been described in either *Acipenser* or *Scaphirhynchus*.

In 1904 I fully described the canals in an adult specimen of *Acipenser sturio*, but I did not attempt to determine definitely the innervation of the related sense organs. The main-infraorbital canal, as shown in the accompanying fig. 11, runs forward from the hind end of the skull, anastomoses first with the lateral end of the supratemporal canal and then with the hind end of the supraorbital, the latter point of anastomosis lying, as in *Polypterus*, at a relatively considerable distance dorso-posterior to the eye. From there the canal curves downward posterior to the eye and passing over the lateral edge of the head reaches its ventral surface approximately lateral to the lateral edge of the transverse opening of the mouth. It then runs forward on the ventral surface of the head somewhat mesial to its lateral edge, passes lateral to the barbels and then turning abruptly mesially anterior to them reaches the lateral

edge of the median subrostral ridge, where it turns abruptly forward along the lateral edge of that ridge and so continues to the end of the snout. There it turns upward across the anterior edge of the snout and then mesially on its dorsal surface to meet in the median line and fall directly into its fellow of the opposite side. At the point where it turns abruptly mesially on to the dorsal surface of the snout a short branch canal is sent dorso-postero-laterally, and as the latero-sensory organs were not traced in the dissection I was unable to

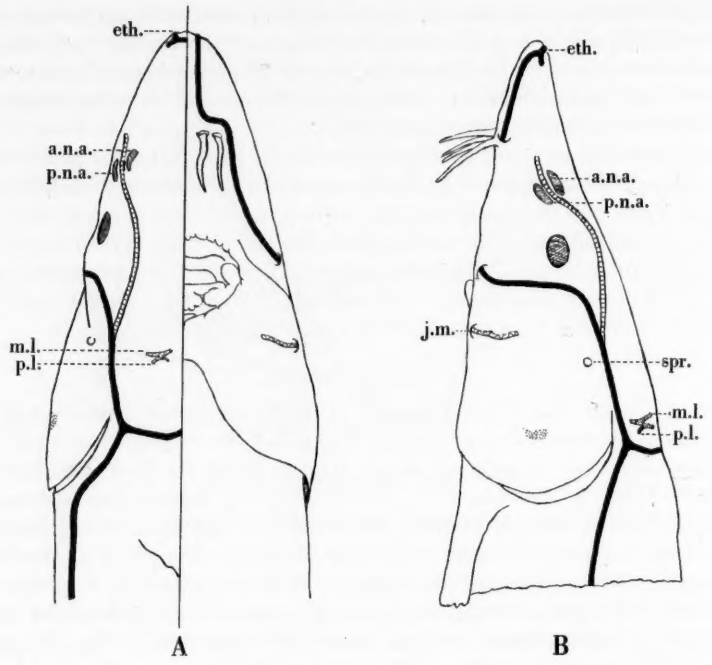

Fig. 11. *Acipenser sturio.* After Allis. *A.* Left side showing dorsal view, right side showing ventral view. *B.* Lateral view.

determine whether this branch was the actual anterior end of the main-infraorbital canal or simply an enlarged primary tubule. Comparing the conditions in this fish with those in *Polypterus* it is evident that the short canal of *Acipenser* corresponds to the slight bulge in that canal of *Polypterus*. This short branch of the canal of *Acipenser* must therefore be the morphologically anterior end of the main-infraorbital canal.

In an advanced larva of *Acipenser ruthenus*, Sewertzoff (1926) shows an ethmoidal canal similar to that in *Acipenser sturio* and calls it the canalis transversus rostri. He says that a short branch canal is given off from the

lateral end of the commissure and that the commissure is entirely enclosed in the cartilage of the snout, as it also is in the adult *Polyodon* (Allis, 1903*b*).

The supraorbital canal of *Acipenser*, starting from its point of anastomosis with the main-infraorbital, runs forward dorsal to the eye and turning antero-ventrally passes between the two external nasal apertures of its side of the head. There it definitely ended in all the adult specimens that I examined, but the line of the canal was prolonged anteriorly by an exposed line of the cartilage of the snout. According to Sewertzoff the canal is here prolonged anteriorly, in *Acipenser ruthenus*, to the anterior end of the snout, but it is not so shown in his figure.

In *Polyodon* (Allis, 1903*b*) and *Scaphirhynchus* (Allis, 1904) the main-infraorbital and supraorbital canals have the same general course that they have in *Acipenser*, but in *Scaphirhynchus* I found no cross-commissural canal between the anterior ends of the main-infraorbitals.

In both *Acipenser* and *Scaphirhynchus* I described on either side of the dorsal surface of the head at about the middle of the length of the parietal two short transverse canals, and as Norris (1925) and Sewertzoff (1926) both have since shown that the anterior one of these two canals is innervated, in *Acipenser*, by the nervus glossopharyngeus and the posterior one by the nervus vagus, it is evident that the two canals are the homologues, respectively, of the middle and posterior head lines of pit organs of *Amia*. These canals have never been described in *Polyodon*.

On the cheek of each of the three fishes here under consideration there is a single latero-sensory canal and it is innervated in each of them by the ramus mandibularis externus facialis. In *Acipenser* and *Scaphirhynchus* the canal is dorso-ventral in position and lies midway between the eye and the base of the gill-cover. It is short, its dorsal end lying slightly below the level of the ventral margin of the eye and its ventral end not quite reaching the level of the angle of the gape, and in *Scaphirhynchus* at about the middle of its length there is a short horizontal canal directed anteriorly. Posterior to it, along the base of the gill-cover, there is a row of little scale-like ossicles which thus have approximately the position of the preoperculum of *Polypterus* and the Holostei and Teleostei, but there was no indication in surface examination of any sense organs related to them. In *Polyodon*, the canal anastomoses by its dorsal end with the main-infraorbital at or near the dorsal end of its postorbital section, and from there runs postero-ventrally ventral to the spiracle, beyond which it curves ventro-anteriorly and extends into the lower jaw but does not reach its anterior end. This canal is evidently the homologue of the preoperculo-mandibular canal of *Chlamydoselachus*, the dorsal end of the canal having simply swung downward and forward to a position intermediate between that it has in *Chlamydoselachus* and that in *Necturus* and the Dipnoi. This canal is therefore quite certainly not the homologue, as I formerly considered probable, of that in *Acipenser* and *Scaphirhynchus*, the latter canal quite certainly being the homologue of the jugal-oralomandibular of *Chlamydoselachus*. The con-

ditions in these Chondrostei thus suggest that they represent two lines of descent from an ancestor in which both cheek lines were present, as they are in *Chlamydoselachus* and *Mustelus*, and that the preoperculo-mandibular line persisted, or at least dominated, in *Polyodon* and the jugal-oralomandibular line in the other Chondrostei; and it is to be noted that in *Polyodon* the mouth opening is approximately terminal in position, as it is in *Chlamydoselachus*, while in the other two Chondrostei it is definitely ventral and transverse in position as it is in most of the recent Plagiostomi.

HOLOSTEI

In these fishes the snout is of viscero-trabeculo-cranial origin and there is no spiracular opening even in early embryos. There is, however, in both *Amia* and *Lepidosteus* a spiracular diverticulum with related sensory organs innervated by a branch of the ramus oticus, and in *Lepidosteus* this organ is considered by Veit (1911) to develop definitely in the endodermal lining of the diverticulum. If this be correct, which seems improbable when compared with the conditions in *Ceratodus* and *Protopterus*, it would strongly suggest that this organ of *Lepidosteus* is of the same character as the sensory organs described by authors in the branchial arches of *Petromyzon* and said by Johnston to be innervated by communis fibres.

In the adult *Amia calva*, as described by me (Allis, 1889) and shown in the accompanying fig. 12, the main-infraorbital canal running forward anastomoses first with the lateral end of the supratemporal canal, then with the dorsal end of the preoperculo-mandibular and still further forward with the penultimate primary pore of the supraorbital canal. The latter point of anastomosis lies close to the dorso-posterior margin of the orbital opening instead of, as in *Polypterus* and *Acipenser*, at a considerable distance posterior to that opening, this evidently being related to the large size of the eyeball. Anterior to this the infraorbital turns sharply downward behind the orbital opening and then forward ventral to it and at the anterior margin of the opening curves upward and anastomoses with the penultimate primary pore of the antorbital section of the canal. The latter section runs downward and forward ventral to the anterior nasal tubule and beyond that tubule turns dorso-mesially and slightly posteriorly on the dorsal surface of the snout and meets in the median line and anastomoses with its fellow of the opposite side. A V-shaped ethmoidal cross-commissural canal is thus formed, the point of the V directed posteriorly, and there is no indication either of the slight swelling in this canal of *Polypterus* or of the short branch that, in the recent Chondrostei, represents the morphologically anterior end of the canal. That part of the canal that lies between its points of anastomosis with the supratemporal and supraorbital canals is innervated partly by the supratemporal branch of the nervus glossopharyngeus and partly by the ramus oticus lateralis, the dorsal organ of the postorbital portion of the canal being innervated by a branch that arises from the preauditory lateralis ganglion close to the base

of the ramus oticus, and the remainder of the canal by branches of the ramus buccalis lateralis.

The supratemporal canal is directed dorso-mesially and meets and anastomoses in the median line with its fellow of the opposite side, and it and the organs of the main line that lie immediately posterior to it are innervated by branches of the supratemporal branch of the nervus vagus.

The supraorbital canal anastomoses by its penultimate primary pore with the main-infraorbital between its horizontal and postorbital portions, and from there runs anteriorly and then antero-latero-ventrally dorso-mesial to the orbital opening, and passing between the two external nasal apertures of its side of the head there ends. Posterior to its point of anastomosis with the main-infraorbital it extends dorso-posteriorly a short distance and is continued onward in that direction by the anterior head line of pit organs, the two lines

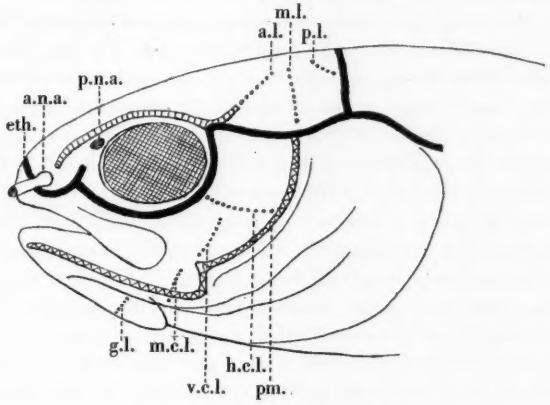

Fig. 12. *Amia calva*. After Allis.

being directly continuous with each other. The canal is innervated throughout its entire length by the ramus ophthalmicus lateralis.

The preoperculo-mandibular canal anastomoses by its dorsal end with the main-infraorbital between the sections of that canal that are innervated by the ramus oticus and the supratemporal branch of the nervus glossopharyngeus, and from there runs downward across the cheek and then forward in the mandible nearly to its anterior end. It is innervated by the ramus mandibularis externus facialis.

On the cheek of the fish there are horizontal, vertical and mandibular lines of pit organs, as shown in the accompanying figure, and they are all innervated by branches of the ramus mandibularis externus facialis. The horizontal line therefore corresponds to the jugal line of the Selachii, and the vertical and mandibular lines, together, correspond to the oralomandibular line of the latter fishes. On each side of the ventral surface of the head there is a gular

line, but its innervation could not be determined. On the dorsal surface of the head there are anterior, middle and posterior head lines of pit organs innervated, respectively, by the ramus ophthalmicus lateralis and the supratemporal branches of the nervi glossopharyngeus and vagus.

In a 10 mm. embryo the suborbital section of the main-infraorbital line runs directly into and is continuous with the thickening of the ectoderm in which the nasal pit develops, this being as described by Platt in a 12 mm. embryo of *Necturus*. The antorbital section of the infraorbital line lies antero-ventral to this connection of the suborbital line with the nasal epithelium, but when the suborbital line separates from this nasal epithelium the antorbital section of the line is extended dorso-posteriorly across the anterior end of the suborbital section and so gives origin to the conditions in the adult. The supraorbital line in these early embryos runs forward to a point dorso-mesial to the nasal pit and there turns abruptly toward that pit, thus having a hook-like anterior end that resembles somewhat that in *Polypterus* but does not approach and anastomose with the ethmoidal canal. The jugal canal extends posteriorly across the cheek from the ventral end of the postorbital section of the infraorbital canal, and the dorsal end of the oralomandibular line closely approaches the anterior end of this jugal line. These two lines thus here have the same relation to each other and to the infraorbital line that they have in Chimaera, but the dorsal end of the oralomandibular line of *Amia* later shifts posteriorly and acquires a position approximately similar to that it has in *Chlamydoselachus*. The dorsal end of the preoperculo-mandibular line of this embryo lies immediately posterior to or slightly ventral to the hind end of the jugal line, but later grows upward and acquires anastomosis with the main-infraorbital. There is no indication in these embryos of a ventral longitudinal line, and it is therefore quite improbable that such a line takes part in the formation of the mandibular part of the preoperculo-mandibular line.

TELEOSTEI

The snout of these Fishes, as shown in a figure given by de Beer (1926, p. 93) is of viscero-trabeculo-cranial origin, and although a spiracle has been said to be present in early embryos of certain of them it is absent in the adult.

The latero-sensory canals have been more or less completely described in many of these Fishes, but for the purposes of this paper it will be sufficient to consider those in *Conger* alone, as described by me (Allis, 1903*a*).

In *Conger conger* (fig. 13) the main-infraorbital canal after anastomosing with the lateral end of the supratemporal continues onward to the dorso-posterior margin of the eye, where it anastomoses with the hind end of the supraorbital. It then turns downward posterior to the eye and forward ventral to it, there entering and traversing a lachrymal bone as in *Amia*. Beyond this bone it, however, turns antero-mesially and slightly dorsally and passing superficial to the anterior nasal passage ends in a pore that lies close to and dorso-mesial to the base of the anterior nasal tube. The anterior organ of this

suborbital portion of the canal lies immediately anterior to the dorso-anterior edge of the lachrymal enclosed in a ring of semi-cartilaginous tissue, and between this ring and the lachrymal the second tube of this part of the line arises and projects antero-ventrally along the base of the anterior nasal tube, thus having the direction of the subnasal (antorbital) portion of the canal of *Amia*. The line of this primary tube is continued by a short line of surface sense organs which leads toward a pore that forms the beginning of the ethmoidal section of the main-infraorbital line. From this pore the ethmoidal canal runs dorso-postero-mesially and enters a median cavity in this part of the skull where it anastomoses with its fellow of the opposite side. Dorso-posterior to the point where this posterior portion of the ethmoidal canal enters the median ethmoidal cavity the anterior section of the ethmoidal canal begins, and running antero-laterally anastomoses with the anterior end of the supraorbital canal, a double tube and pore apparently being formed at the point of anastomosis.

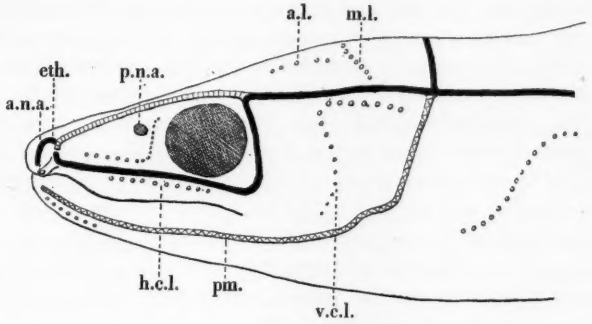

Fig. 13. *Conger conger*. After Allis.

The ethmoidal canal of this fish is thus a short U-shaped canal that fuses at the summit of the U with the corresponding part of the canal of the opposite side of the head, thus being strictly comparable to the U-shaped ethmoidal (internasal) bend in the main-infraorbital canal of *Chlamydoselachus* excepting that, in *Conger*, it lies on the dorsal instead of on the ventral surface of the head. It is therefore quite probable that the ethmoidal cross-commissures of *Acipenser*, *Polyodon* and *Polypterus* are developed in this same manner, the cross-commissures in *Amia* and *Lepidosteus* apparently being comparable to the internasal anastomosis of the canals in *Raia* rather than to that in *Chlamydoselachus*.

The supraorbital canal anastomoses by its hind end with the main-infraorbital at the bend between its horizontal and postorbital portions, and from there runs forward dorso-mesial to the eye and to both nasal apertures of its side of the head and anastomoses by its anterior end with the anterior end of the ethmoidal canal in the manner just above described. In the others

of the Muraenidae described by me (Allis, 1903*a*), the conditions are here similar to, but simpler than those in *Conger*, and in *Scomber* the conditions are still simpler, the ethmoidal canal being there represented by that short anterior section of the supraorbital canal that lodges the one organ that I found to be innervated by the ramus buccalis (Allis, 1903*c*). I, at the time, considered this condition in *Scomber* exceptional and abnormal, but it simply means that the ethmoidal canal lodges but a single organ and that this section of the canal does not anastomose in the median line with its fellow of the opposite side.

The preoperculo-mandibular and supratemporal canals of *Conger* are strictly similar to those in *Amia*, but in *Conger* they anastomose with the main-infraorbital directly opposite each other.

I described in this fish what I considered to be anterior and middle head lines of pit organs, but the innervation of the anterior line by a nerve that issues from the skull between the frontal and parietal bones would seem to indicate that it is a branch of the nervus glossopharyngeus rather than of the ramus ophthalmicus lateralis, and if this be so the two lines would be middle and posterior instead of anterior and middle ones. There are also horizontal and vertical cheek lines and a mandibular line, but the horizontal cheek line has shifted so far forward that it lies ventral to and parallel to the suborbital portion of the main-infraorbital canal. The innervation of these cheek lines was not definitely determined but is quite certainly the same as that of the corresponding lines in *Amia*. There is furthermore a line of these surface organs that lies ventral to and parallel to the horizontal portion of the main-infraorbital canal and as it was apparently innervated by the nervus glossopharyngeus, and as there was no organ innervated by that nerve in the main canal, I concluded that the pit organs had probably replaced the missing canal organ. Immediately anterior to the eye, between it and the posterior nasal aperture, there is a vertical line of these same surface organs which, at its ventral end, turns abruptly forward and extends nearly to the base of the anterior nasal tube. It is innervated by an independent branch of the ramus ophthalmicus lateralis and at its dorsal end closely approaches the supraorbital canal. If it were to anastomose with that canal it would strikingly resemble the so-called ethmoidal canal of Bromer's descriptions of embryos of *Spinax niger*, called by Ruud the ventral section of the supraorbital canal. A similar line of pit organs is found both in *Esox* and *Ameiurus* (Allis, 1904), and in *Esox* the horizontal cheek line has shifted forward ventral to the eye as it has in *Conger*.

Posterior to the preopercular canal, on the lateral surface of the gill-cover, there is a line of surface organs that are somewhat smaller than the organs on the cheek, but their innervation was not determined. Herrick (1899) has described in *Menidia* a single organ that apparently represents this line. It lies posterior to the dorsal third, approximately, of the preopercular canal and hence in a position that corresponds to the short branch that, in *Chlamydoselachus*, projects posteriorly from the preoperculo-mandibular line at about

its dorsal third and lodges one sense organ. In *Menidia* this organ is innervated by a nerve that Herrick calls the ramus opercularis superficialis facialis, and this nerve is prolonged ventrally to innervate four organs that lie in a horizontal line near the ventral edge of the gill-cover, thus having the position of what is called in *Petromyzon* and *Necturus* the hypohyal portion of the ventral longitudinal line. If these organs actually belong to this part of the ventral line it is evident that the mandibular part of the preoperculo-mandibular line of this fish and also others of the Teleostei is definitely an anterior prolongation of the ventral end of the preoperculo-mandibular line, as it is in *Ceratodus*, and not a part of the ventral longitudinal line, as it is in *Necturus* and *Protopterus*.

In most others of the Teleostei the main-infraorbital canal extends only to the anterior end of the bone called the lachrymal, but it may be continued onward over the top of the snout by a line of surface organs. The preoperculo-mandibular canal may, or may not, anastomose by its dorsal end with the main-infraorbital, that anastomosis when it takes place always being with the main-infraorbital between its preauditory and postauditory portions. In most of these fishes the supraorbital canal runs forward dorso-mesial to the eye and the nasal apertures and there ends, but in *Batrachus tau* it is said by Clapp (1898) to turn antero-laterally at its anterior end and pass between the nasal apertures and there end, as it does in the Chondrostei and Holostei. At the point where in *Batrachus tau* the hind end of this canal bends abruptly laterally behind the eye to join the main-infraorbital between its horizontal and postorbital portions, the supraorbital canals of opposite sides are connected by a short commissural vessel which arises from each canal between two adjacent sense organs. There is no organ in the commissural vessel and no surface pore related to it and it is accordingly quite certainly formed by the anastomosis of two primary tubes. In *Gadus morrhua* (Cole, 1898) the supraorbital canals are similarly connected by a short commissural vessel, but from the median point of the commissure a tube projects posteriorly and opens on the external surface by a single median pore.

OSTRACODERMI

Osteostraci

In these pre-Fishes the snout is of the viscero-trabeculo-cranial type (Allis, 1931 *b*) and the general course of the latero-sensory canals is considered to be indicated by narrow and shallow grooves on the dorsal surface of the cephalic shield, and these grooves vary considerably in different specimens and even on opposite sides of the head of the same specimen. They are particularly described by Stensiö (1927) in *Benneviaspis holtedhali* and *Hoelaspis angulata* and as shown by him in *Benneviaspis* are reproduced in the accompanying fig. 14. On the right-hand side of this figure, what I consider to be the main-infraorbital line begins at the hind edge of the cephalic shield and extends

from there antero-dorsally to the dorso-posterior border of the orbital opening, being represented throughout this part of its course by four short and wholly independent grooves. The antero-dorsal one of these grooves would seem quite certainly to represent the oticus section of the main-infraorbital, but Stensiö considers it to correspond to the middle head line of pit organs of recent Fishes. Slightly anterior to its anterior end a short groove begins and extends latero-ventrally behind the orbital opening, thus having to that opening definitely the position of a postorbital section of the main-infraorbital line. It is however considered by Stensiö to correspond to what he calls the suprapineal lateral line organs of *Petromyzon*, which latter organs would seem to be what I have described in that cyclostome as the supraorbital line. Slightly anterior to the latero-ventral end of this line another groove begins and extending from there antero-latero-ventrally a relatively considerable distance evidently represents the suborbital and antorbital portions of the

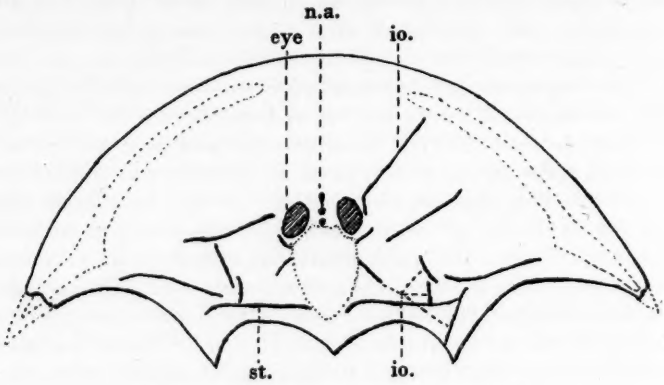

Fig. 14. *Benneviaspis holtedhali*. After Stensiö.

main-infraorbital. In *Trematapis*, the anterior end of this line is said by Patten (1903) to curve antero-mesially and closely approach its fellow of the opposite side. There it turns postero-mesially and together with its fellow of the opposite side forms a median V-shaped groove which suggests the ethmoidal canal of *Amia*. Stensiö says that the anterior portion of this canal of *Trematapis* may have been innervated by the ramus ophthalmicus profundus, which would seem to imply that he has either confirmed or simply accepted Johnston's statement that what I consider to be the anterior section of the main-infraorbital sensory line of *Petromyzon* is innervated by the ramus ophthalmicus profundus.

Near the hind edge of the cephalic shield there is a groove directed dorso-mesially from what I consider to be the main-infraorbital line slightly anterior to its hind end, and it quite certainly represents the supratemporal line as Stensiö suggests. It does not meet in the middorsal line its fellow of the

opposite side. Slightly anterior to its lateral end, but on the opposite side of the main-infraorbital line, a relatively long groove begins and extending from there latero-ventrally would seem, although not so considered by Stensiö, to represent a preopercular line. Half-way between this line and the suborbital portion of the infra-orbital there is a short groove directed antero-laterally which Stensiö considers to correspond either to the preopercular or jugal line of Fishes.

There is no indication in *Benneviaspis* of a supraorbital line.

Heterostraci

In the Pteraspidae the snout is quite certainly of the trabeculo-cranial and not of the viscero-trabeculo-cranial type, for the two nasal apertures, one on either side of the head, are said to lie on the ventral surface of the snout close together and slightly in front of the mouth.

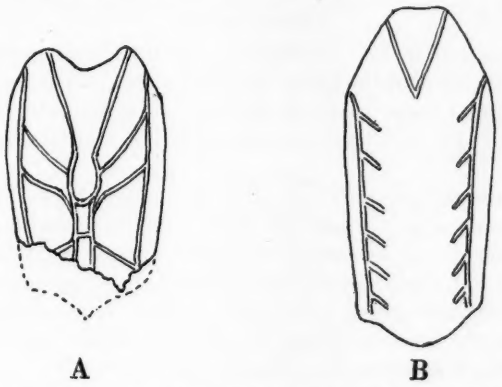

Fig. 15. *Pteraspis crouchi*. A, dorsal view. B, ventral view. After Stensiö.

There are, according to Stensiö (1926), in both *Pteraspis* and *Palaeaspis* three longitudinal latero-sensory canals on each side of the head, two on its dorsal and one on its ventral surface (fig. 15), and they apparently correspond to the three longitudinal ectodermal ridges described by Platt in embryos of *Necturus* and called by her the dorso-lateral, epibranchial and ventral ridges. The dorso-lateral and epibranchial canals both of *Pteraspis* and *Palaeaspis* are connected by transverse canals which apparently correspond to the dorsal portions of the intersegmental ectodermal ridges of embryos of *Necturus*. In *Palaeaspis* all of these intersegmental lines are prolonged dorso-mesially to meet in the median line their fellows of the opposite side, while in *Pteraspis* the anterior one of these lines is not so prolonged. In *Palaeaspis* the anterior one of these transverse canals is prolonged ventrally posterior to the eye, thus there having a position that corresponds to that of the postorbital canal of Fishes and also to the anterior one of the intersegmental lines of embryos of

Necturus and *Ceratodus*. Its course beyond the lateral edge of the dorsal surface of the head is not known. The dorso-lateral longitudinal canal is prolonged anteriorly beyond this transverse canal to the anterior edge of the snout, thus corresponding to the supraorbital prolongation of the dorso-lateral ridge of *Necturus*, and it is considered by Stensiö to represent the supraorbital canal. Whether it extended onward on to the lateral and ventral surfaces of the head is unknown. The ventral canals of opposite sides lie each near the lateral edge of the ventral plate, and between their anterior ends there is a V-shaped median canal that would seem to correspond to the median V-shaped canal on the ventral surface of the head of *Protopterus*. Stensiö, however, suggests that it may correspond to the circumbuccal canal of *Petromyzon* and he furthermore considers the latero-sensory canals of these pre-Fishes to correspond to those in the Petromyzontidae, but they would seem to resemble more closely those in embryos of *Ceratodus* and *Necturus*.

ARTHRODIRA

These Fishes are separated by Stensiö into Macropetalichthyids and non-Macropetalichthyids, and the latero-sensory canals in these two groups differ markedly in certain respects not only from each other but also from the canals in recent Fishes. The conditions in the non-Macropetalichthyids will be first considered.

In *Coccosteus decipiens* the course of the latero-sensory canals is said to be indicated by grooves on the external surfaces of the dermal bones that form the cephalic shield, and as recently described and figured by Heintz (1931) they are, with but slight modification, shown in the accompanying fig. 16. Stensiö described and figured these canals in 1925, but in his figure giving a lateral view of the head of the fish he followed Jaekel's reconstruction, and Heintz says that it is incorrect in certain particulars.

The main-infraorbital canal begins at the hind edge of the cephalic shield and running forward immediately gives off a branch which extends dorso-antero-mesially and is evidently the supratemporal, as Stensiö concludes. In the figure given by Heintz and above referred to, this canal is shown prolonged dorso-antero-mesially until it meets and becomes continuous with the ventro-lateral end of the posterior head line, but this seems exceptional, for Stensiö in his figure shows it ending considerably postero-ventro-lateral to this head line, as does also Heintz in certain other figures that he gives of this fish. I have accordingly so shown it in the accompanying figure. Beyond this supratemporal branch the main-infraorbital turns sharply antero-latero-ventrally and so continues in a nearly straight line until it reaches a point considerably posterior to the orbital opening and approximately in the horizontal level of the middle of the height of that opening. There it sends a branch postero-latero-ventrally to the latero-ventral edge of the cephalic shield, and itself turning sharply anteriorly and slightly dorsally so continues until it reaches the dorso-posterior margin of the orbital opening where it

anastomoses with the ventral end of what I shall call the posterior division of the supraorbital canal. Beyond this branch it turns ventro-anteriorly behind the orbital opening and then forward ventral to it, and as shown by Heintz ends slightly beyond that opening, there lying somewhat ventral to the anterior end of the supraorbital. Stensiö, however, says that the canal probably continued onward beyond this to the anterior edge of the cephalic shield. At the postero-ventral border of the orbital opening a branch is sent postero-ventrally to the angle of the gape but apparently does not there turn forward into the mandible. This branch canal is evidently the jugal, the branch sent postero-ventrally from the middle of the length of the horizontal part of the main-infraorbital apparently being the preopercular, this being in accord with Stensiö's conclusions.

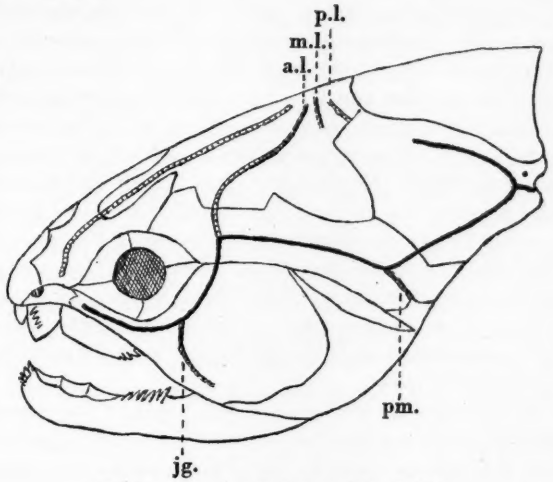

Fig. 16. *Coccosteus decipiens.* After Heintz.

What I have above referred to as the posterior division of the supraorbital canal arises from the main-infraorbital between its horizontal and postorbital portions, and running at first dorso-postero-mesially and then mesially approaches but does not actually meet in the middorsal line its fellow of the opposite side. Stensiö considers this canal to represent either the anterior head line of recent fishes or to be a dorso-mesial prolongation of the postorbital section of the main-infraorbital similar to that described by Ewart in *Laemargus*, and he favours this latter view. It is, however, to be noted that in *Laemargus* the anterior end of the horizontal section of the main-infraorbital curves upward and is prolonged dorsally to the same extent as the postorbital section of the canal, there thus not being any actual prolongation of the latter section of the main-infraorbital. If this canal were a prolongation of the postorbital portion of the main-infraorbital, it must have been innervated by the ramus

buccalis, and no branch of this nerve extending dorsally beyond the level of the horizontal portion of the main-infraorbital is known in recent Fishes. Furthermore, the postorbital portion of the main-infraorbital of *Ceratodus* is said by Greil to be developed in relation to that part of the mandibulo-premandibular intersegmental line that lies ventral to the epibranchial line, and it could not accordingly primarily have extended dorsally beyond that line. It therefore seems quite certain that this branch canal was innervated by the ramus ophthalmicus lateralis. Slightly posterior to its dorsal end there are two short canals which evidently represent the middle and posterior head lines of recent Fishes, as Stensiö concludes. This strongly suggests that the dorsal portion of the branch canal is an anterior head line, the ventral portion of the branch canal then probably being a postanastomosis portion of the supraorbital canal similar to that in *Amia* and probably also in *Protopterus*. To give origin to the conditions in *Coccosteus*, the preanastomosis portion of a primarily continuous line would simply have had to become segmented from the postanastomosis portion and then have shifted somewhat dorsally. That the branch canal is simply an anterior head line seems improbable, for this head line never, in any of the recent Fishes considered, anastomoses directly with the main-infraorbital. Furthermore, it is to be noted that excepting in *Polypterus* and possibly also in *Conger* an anterior head line is not described in any of the recent Fishes considered when the supraorbital canal anastomoses by its hind end with the main-infraorbital. Because of this, and also because of the evident presence of an anterior head line in *Coccosteus*, it seems improbable that the branch canal of this fish is simply a posterior but preanastomosis portion of the supraorbital canal similar to that in the Macropetalichthyids, described immediately below.

The anterior division of the supraorbital canal of *Coccosteus*, as above defined, begins slightly anterior to the dorso-mesial end of its posterior division and from there runs antero-ventrally dorsal to the orbital opening and beyond that opening turns ventrally between it and the nasal opening and is said by Stensiö to approach closely and probably anastomose with the main-infraorbital. In my fig. 16 it should have been shown extending slightly farther ventrally.

In *Dinichthys halmodeus* the latero-sensory lines, as shown by Stensiö (1925*b*) in dorsal view, are strictly similar to those in *Coccosteus*, but Heintz (1932) in his figure of this fish does not show the middle and posterior head lines. In *Phlyctenaspis acadica*, another of the non-Macropetalichthyids described by Stensiö (1925*b*), the supraorbital canal presents the same two subdivisions that it does in *Coccosteus*, but there are no indications either of middle or posterior head lines. There are also no supratemporal and jugal canals.

In each of these three Fishes there is on either side but a single nasal perforation of the cephalic shield, and if there were in either of them two external nasal apertures the separation of the primitive single opening into

two must have taken place wholly in the dermal tissues that overlay the cephalic shield. The anterior end of the supraorbital canal must have lain directly upon the external surface of the dermal cranial shield as indicated by the groove that marks its course. It must therefore have lain posterior to a so-developed single nasal aperture, or posterior to a posterior aperture that would have resulted from its subdivision into two, and this relation of this canal to either of these apertures, while it apparently also occurs in certain of the Palaeoniscidae (*Cheirolepis, Perleidus*), is unknown in the recent Fishes considered excepting only the Elasmobranchii, where the nasal aperture of either side lies on the ventral surface of the snout and has not undergone complete subdivision. When a primarily single nasal aperture has undergone subdivision before the supraorbital line has grown antero-ventrally beyond the horizontal line of the nasal opening, a barrier is placed across the path of the line and it either grows forward on to the nasal bridge and hence between the two external nasal apertures, or runs forward dorso-mesial to both apertures, as in *Osteolepis* and most of the recent Teleostei. The position of this canal in *Coccosteus* would thus seem to be primitive, as compared with that in *Macropetalichthys* and in most of the recent Teleostomi.

In *Macropetalichthys rapheidolabis* (fig. 17) the latero-sensory canals differ markedly in certain respects from those in *Coccosteus*. The chondrocranium of this fish, as described by Stensiö (1925*b*), resembles in many respects that of *Polyodon folium* as described by Bridge (1878). The nasal capsules project laterally from the lateral surfaces of the ethmoidal region, but the external opening of each capsule is directed latero-ventrally instead of, as in *Polyodon*, latero-dorsally. On the ventral edge of the opening there is in *Macropetalichthys* a small process projecting dorsally and indicating a separation of the opening into anterior and posterior portions, the anterior one of which is considered by Stensiö to represent the external nasal opening and the posterior one to correspond to what I (Allis, 1923) described in *Chlamydoselachus* as the nasal fontanelle. A small process on the ventral edge of the nasal opening of *Polyodon* similarly indicates a separation of that opening into two parts, and Bridge says that these two portions of the opening represent definitely the anterior and posterior nasal apertures, and this is quite certainly the proper interpretation of the conditions in *Macropetalichthys* also. Between the nasal capsules of opposite sides there is in *Macropetalichthys* a relatively large median depression that Stensiö considers to represent the cavum precerebrale of my descriptions of *Chlamydoselachus*. In an earlier work (Allis, 1931*c*) I suggested that this depression might simply represent the point where the naso-hypophysial canal primarily had its attachment to the ectoderm, but this seems incorrect.

The labyrinth region of the chondrocranium is short and broad, and near its hind end there is a pit-like depression at the bottom of which there is a foramen leading into the cranial cavity, and Stensiö considers this foramen to have given passage to the ductus endolymphaticus. In *Polyodon* there is a strictly

similar pit-like depression, and Bridge considered it also to have given passage to the same duct. In drawings that I have of dissections of *Polyodon* made some ten years ago by my former assistant Mr John Henry, the foramen at the bottom of this pit is however shown to be completely closed by the thick lining membrane of the cranial cavity, and the ductus endolymphaticus lies a relatively considerable distance anterior to this and there is no perforation of the cranial roof related to its dorsal end. This depression of *Polyodon* is apparently the homologue of the pre-epiotic fossa of Ridewood's (1904) descriptions of the Clupeidae. The external opening of the fossa of *Polyodon* lies antero-lateral to the posterior semicircular canal, while the foramen at the bottom of the fossa lies postero-mesial to that canal. The endolymphatic duct, if it traversed this fossa, would accordingly have had to pass through the arch of the posterior semicircular canal, which seems wholly improbable. What the relations of the fossa of *Macropetalichthys* are to the posterior semicircular canal cannot be told from the descriptions. It lies immediately anterior to a latero-sensory canal that Stensiö considers to be the supratemporal, while the

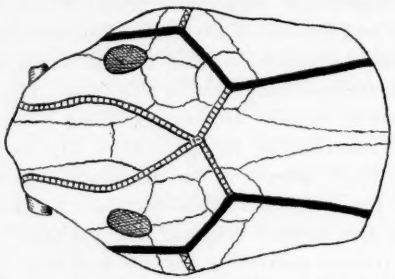

Fig. 17. *Macropetalichthys rapheidolabis*. After Stensiö.

fossa of *Polyodon* lies immediately posterior to the laterally curving hind end of the supraorbital canal. In *Epipetalichthys* there is a perforation of the cephalic shield that is said by Stensiö to lead into a similar pit, and it lies posterior to the so-called supratemporal canal.

The occipital region of the chondrocranium is long and slender, as it is in *Polyodon*, and at its hind end there is on either side a lateral occipital process called by Stensiö the cranio-spinal process and by Bridge the decurrent wing-like process. In *Saurichthys ornatus* (Stensiö, 1925*a*) the postorbital and occipital regions have the same general shape as in the two above-mentioned fishes and the hind ends of the dermal bones that cover the dorsal surface of the chondrocranium in each of them rest upon the dorsal surfaces of the lateral occipital processes. The chondrocranium of *Macropetalichthys* would accordingly seem to resemble that of *Polyodon* much more than it does, as Stensiö concludes, that of the Selachii.

The main-infraorbital canal of *Macropetalichthys* begins at the hind edge of the cephalic shield and from there runs forward in a longitudinal direction

until it reaches a point that lies slightly anterior to the hind edge of the dorsal surface of the preoccipital portion of the chondrocranium and at about half way between the hind edge of the cephalic shield and the orbital opening. There it anastomoses with the postero-lateral end of a canal that Stensiö considers to be the supratemporal, and itself turns antero-ventro-laterally at a sharp angle and so continues until it reaches a point that lies somewhat posterior to the ventral border of the orbital opening. There it gives off a branch which extends latero-ventrally and but slightly posteriorly to the latero-ventral edge of the cephalic shield and is considered by Stensiö to be the preopercular canal. The main-infraorbital then turns sharply forward ventral to the orbital opening and slightly beyond that opening passes over the lateral edge of the cephalic shield, this point lying at a relatively considerable distance posterior to the nasal capsule. The branch canal, above referred to, that Stensiö considers to be the supratemporal, runs dorso-antero-mesially and meets in the middorsal line and anastomoses both with its fellow of the opposite side and with the fused hind ends of the so-called supraorbital canals of opposite sides of the head. These latter canals immediately separate from each other and each canal runs forward mesial to the orbital opening and dorsal to the nasal capsule and reaches the anterior edge of the cephalic shield, curving slightly antero-laterally as it approaches that edge. Beyond this it entered the soft tissues of the snout and could not be further traced, but Stensiö suggests that it there turned posteriorly, repassed dorsal to the nasal capsule and fell into the main-infraorbital between that capsule and the orbital opening, as it does in the Selachii.

In *Epipetalichthys wildungensis*, also described by Stensiö, the general course of the canals is strictly similar to that in *Macropetalichthys*, but the hind ends of the so-called supraorbital canals do not anastomose either with each other or with the so-called supratemporal cross-commissure. Each of these so-called supraorbital canals therefore begins independently slightly anterior to the so-called supratemporal commissure and from there runs forward to the anterior end of the cephalic shield, there passing so close to the external opening of the nasal capsule that it would seem improbable that it could have had a recurrent course dorsal to the capsule. Neither preopercular nor jugal canal is shown in the figure.

Comparing the conditions in these two Macropetalichthyids with those in certain of the teleosts above considered it seems quite certain that the canal called by Stensiö the supratemporal is the homologue of that part of the supra-orbital canal of *Batrachus tau* (Clapp, 1898) and *Gadus morrhua* (Cole, 1898) that lies posterior to the point where the supraorbitals of opposite sides are connected with each other by a short commissural vessel. This transverse commissure in these two fishes is certainly formed by the anastomosis of two primary tubes, one belonging to each of the two supraorbital canals, and if these tubes were to be reduced in length so that the anastomosis was by primary pores instead of by primary tubes, the conditions in *Macropetalichthys* would

arise; and this shortening of primary tubes and the ultimate anastomosis by primary pores is what actually takes place in *Amia* where the penultimate pore of the supraorbital anastomoses with the main-infraorbital between its horizontal and post-orbital portions. The conditions in *Epipetalichthys* would then arise from those in *Macropetalichthys* if those portions of the supraorbital canals that lie anterior to their point of fusion with each other were to be pinched off from the posterior portions. That the conditions in *Macropetalichthys* could have been derived directly from those in *Coccosteus* by the swinging forward of the posterior division of the supraorbital canal and its fusion with the hind end of the anterior division seems improbable, but not impossible, for this would apparently give origin to the conditions in *Polypterus*, where the anterior head line anastomoses with the supraorbital a considerable distance anterior to its hind end.

If the above conclusions are correct it is evident that there either was no supratemporal commissure in *Macropetalichthys* or that it was there represented by surface organs that have left in the fossil no trace of their presence. In both *Polyodon* and *Saurichthys*, where the occipital portion of the skull closely resembles that in *Macropetalichthys*, this canal is present and there lies superficial to the hind end of the cephalic shield and approximately directly above the lateral occipital process of its side of the head. If the supratemporal canal had this position in *Macropetalichthys*, the postorbital section of the main-infraorbital canal would be innervated by the ramus buccalis instead of, as Stensiö concluded, by the nervus glossopharyngeus, and the preopercular canal of his determination would be the jugal, this being in accord with what I was led to conclude for other reasons in an earlier work.

CROSSOPTERYGII

In these Fishes the snout is quite certainly of the viscero-trabeculocranial type, for although there is question as to the existence and positions of the external nasal apertures it seems quite certain that there were two of them on each side of the head, and that they lay on its dorsal surface. In *Eusthenopteron fordii* and *Dictyonosteus arcticus* Stensiö (1922) shows a single nasal opening on each side of the head bounded dorsally by a nasal bone and ventroposteriorly by an antorbital, these two bones being in contact or fused with each other behind the opening but diverging forward from there. In *Axelia* (Stensiö, 1921) these two bones completely surround the nasal opening and a narrow bridge of bone has grown across what was probably primarily a single opening and separated it into two. There were thus certainly in the latter fish anterior and posterior external nasal apertures in the dermis on the dorsal surface of the head, and this makes it exceedingly probable that there were two such apertures in other members also of this group. Goodrich (1919) considers the position of the posterior one of these two apertures of *Osteolepis macrolepidotus* to be indicated by a notch in the incurved ventral edge of the dermal bones that cover this part of the snout, while Watson (1925) describes

in this fish, and Watson and Day (1916) describe in *Glyptopomus* what they consider to be an internal nasal aperture lying in the roof of the buccal cavity and similar to that in the Stegocephalia.

The latero-sensory canals of these fishes have been most completely described by Goodrich in *Osteolepis*, and as shown by him are reproduced in the accompanying fig. 18. The main-infraorbital begins at the hind edge of the lateral extrascapular (supratemporal, tabulare) and from there runs forward to the dorso-posterior margin of the orbital opening. There it anastomoses with the hind end of the supraorbital and then turns downward posterior to the orbital opening and forward ventral to it and is shown extending nearly to the anterior end of the lachrymal bone. As it traverses the lateral extrascapular it anastomoses with the lateral edge of the supratemporal canal, that canal meeting in the middorsal line and fusing with its fellow of the opposite side.

The supraorbital canal anastomoses by its hind end with the main-infraorbital between its horizontal and postorbital sections and from there runs

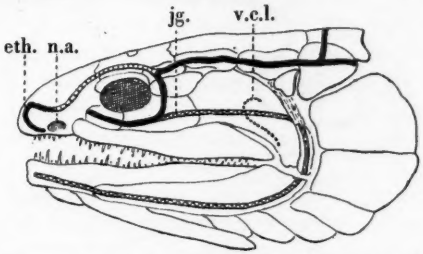

Fig. 18. *Osteolepis macrolepidotus*. After Goodrich.

forward dorso-mesial to the orbital and nasal openings. As it approaches the anterior end of the snout it curves at first antero-mesially and then latero-posteriorly, thus describing a large U-shaped bend that strikingly suggests the U-shaped ethmoidal canal of *Conger* and *Chlamydoselachus*, but the summit of the bend does not, in *Osteolepis*, even closely approach the summit of the bend in the canal of the opposite side. Whether it be this ethmoidal canal or a hook-like bend of the anterior end of the supraorbital similar to that in *Polypterus*, can of course not be definitely determined without knowing the innervation, but in favour of its being a detached portion of the anterior end of the infraorbital canal similar to that in *Conger* is the fact that a cross-commissural ethmoidal canal is described by Stensiö in both *Axelia* and *Eusthenopteron*. The presence of this ethmoidal canal as a U-shaped bend in *Osteolepis* would apparently account for the double row of latero-sensory pores described by Pander (1860) concentric with the anterior edge of the snout of this fish. It is accordingly shown in the accompanying figure as a detached portion of the main-infraorbital.

There are jugal and preoperculo-mandibular canals, as fully discussed in

one of my earlier works (Allis, 1928), and an **S**-shaped line on the so-called squamosal (postorbital) bone apparently represents the vertical cheek line of *Amia*.

CHONDROSTEI

In *Cheirolepis trailli* (fig. 19), one of the Palaeoniscidae described by Watson (1925), the main-infraorbital runs forward until it reaches a point considerably dorso-posterior to the orbital opening, there lying in a bone called by Watson the intertemporal. There a short branch canal is shown extending antero-dorsally to the dorso-mesial edge of the intertemporal, this suggesting a posterior division of the supraorbital canal similar to that above described in *Epipetalichthys*. Anterior to this branch the canal first runs antero-ventrally till it reaches the middle of the post-frontal bone where it turns downward posterior to the orbital opening and then forward ventral to it and ends in a bone that lies immediately anterior to the orbital opening and is called by Watson the lachrymal, the canal there being represented by two

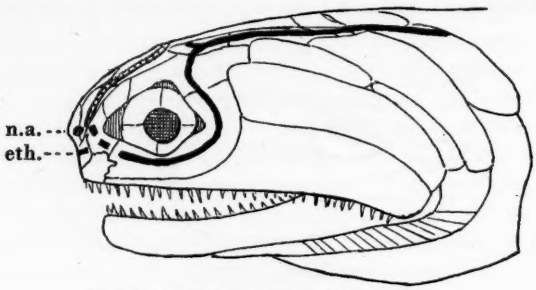

Fig. 19. *Cheirolepis trailli*. After Watson.

short independent sections. The ventral portion of this lachrymal bone articulates anteriorly with a bone called by Watson the rostral, in which an independent anterior division of the main-infraorbital begins, and running antero-mesially meets in the median line and anastomoses with its fellow of the opposite side. This independent section of the main-infraorbital of this fish thus corresponds to the antorbital and ethmoidal portions, together, of the canal of *Amia*, and the so-called rostrals of opposite sides of the head together with the median anterior postrostral of Watson's descriptions must either be or at least contain the homologues of the antorbital and ethmoidal bones of *Amia*. The supraorbital canal begins in the parietal with a free hind end and from there runs forward in that bone and then in the frontal at the anterior end of which it enters a bone that Watson calls the antorbital or nasal and ends near the anterior end of that bone, there lying immediately posterior to the single nasal perforation of the dermal cranial shield. This so-called antorbital cannot therefore be a bone comparable to the antorbital of *Amia*, and it seems quite certain that it must be or at least contain the homologue of the nasal bone of the latter fish. No supratemporal canal is shown by Watson in his figure

giving a lateral view of the head of this fish, but it is shown in a figure giving a dorsal view. Neither preopercular nor jugal canals are shown or described by Watson, but the preopercular canal is probably present, as fully described by me in one of my earlier works (Allis, 1928).

In *Birgeria groenlandica*, which is also one of the Palaeoniscidae, Stensiö (1932) shows the anterior nasal aperture lying in the sutural line between two bones that he calls the postrostral and the nasal, the latter bone being index-lettered Ant. in the figures given. The so-called nasal is a large triangular bone with the pointed end of the triangle directed dorso-posteriorly, and between its hind edge and the anterior edge of the orbital opening there is a small depression which Stensiö considers to represent the posterior nasal aperture. In both *Amia* and *Polypterus* there is a similar break in the dermal bones with a related depression, and the posterior nasal aperture lies in the dermal tissues directly above the depression. The posterior nasal passage leading from this aperture to the nasal capsule lies superficial to the dermal bones and there is no passage leading from the depression itself into the nasal capsule (Allis, 1932 *a*). The depression is accordingly in these two recent Fishes in no sense a posterior nasal aperture and this probably is the condition also in *Birgeria*. The anterior end of the supraorbital canal turns downward in the so-called nasal bone and passing posterior to what Stensiö considers to be the anterior nasal aperture ends near the ventral edge of the bone without falling into the main-infra-orbital, which latter canal traverses a bone lying ventral to the nasal and called by Stensiö the antorbital.

In *Perleidus woodwardi* (fig. 20), one of the Catopteridae described by Stensiö (1921), the main-infraorbital canal runs forward to a point considerably dorso-posterior to the orbital opening and there turns downward behind and forward ventral to that opening. Anterior to the opening it enters a short bone that forms a direct anterior prolongation of the single suborbital bone and is called by Stensiö the rostral. There it anastomoses either directly or through the intermediation of primary tubes with the anterior end of the supraorbital canal, and then enters a median bone called by Stensiö the nasalo-postrostral, where its turns dorso-postero-mesially and meets and anastomoses in the median line with its fellow of the opposite side. A large V-shaped ethmoidal cross-commissure is thus here formed which evidently corresponds to the cross-commissure of *Amia*. The so-called nasalo-postrostral bone must therefore at least contain the homologue of the median dermal ethmoid of *Amia*, and as there is question as to its containing any part of the nasal, it will hereafter be referred to as the dermal ethmoid. The bone called by Stensiö the rostral would then be the antorbital and a bone in just this position in *Birgeria* is so designated by him, as just above stated.

The supraorbital canal begins in the parietal and is said to be prolonged posteriorly by a groove which Stensiö considers to represent the anterior head line. From there the canal runs forward without anastomosing with the main-infraorbital, and after traversing the frontal turns downward anterior to the

orbital opening and enters and traverses a bone called by Stensiö the ant-orbital, at the ventral edge of which it is said to anastomose either directly or through the intermediation of primary tubes with the main-infraorbital as that bone traverses the so-called rostral (antorbital).

The so-called antorbital bone of this fish has exactly the relations to the latero-sensory canals and to the orbital and nasal openings that the nasal bone of Stensiö's later descriptions of *Birgeria* has, and it is quite unquestionably the homologue of that bone. It forms the anterior boundary of the orbital opening, articulates ventrally with the so-called rostral (antorbital) and dorso-anteriorly with the so-called nasalo-postrostral (median dermal ethmoid) and the two nasal openings described by Stensiö lie in the sutural line between it and the latter bone. It is topographically the equivalent of the bone that I have called the nasal in *Cheirolepis* (antorbital, Watson) together with the dorsal

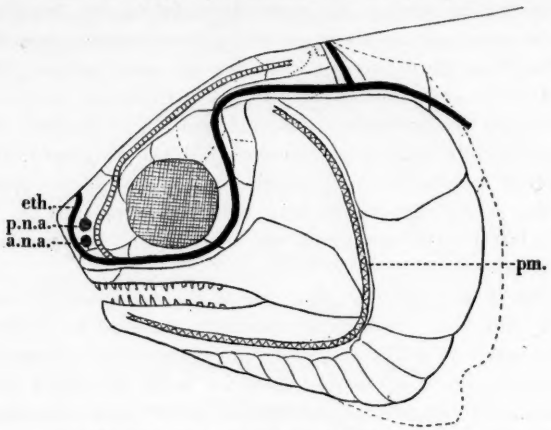

Fig. 20. *Perleidus woodwardi*. After Stensiö.

half of the lachrymal of that fish. There is accordingly question as to the homologies of these several bones.

There is a preoperculo-mandibular canal and a supratemporal cross-commissure in typical positions, and between the latter cross-commissure and the anterior head line there are said to be posterior and middle head lines.

In *Saurichthys ornatus* (fig. 21), as described by Stensiö (1925 *a*), the main-infraorbital canal begins at the hind end of a bone that apparently corresponds to the supraclavicular of my descriptions of *Amia* and *Polyodon*, but it is called by Stensiö the supracleithral. Running forward in this bone it enters a bone called by him the suprascapular and then the supratemporo-intertemporo-extrascapular, in which it continues onward to the anterior end of that bone, which end lies slightly dorso-mesial to the hind edge of the orbital opening. There it turns downward behind that opening and traverses first the hind end of what he calls the dermosphenotic and then two bones called by him

the infraorbitals 1 and 2 which correspond to the latero-sensory components of the postorbital and suborbital bones of *Amia*. Beyond this the canal traverses bones called by Stensiö the lachrymal and nasalo-antorbital there passing ventral to the two nasal apertures and anastomosing with the anterior end of the supraorbital which passes downward between those apertures. Beyond the nasalo-antorbital the canal enters the rostralo-premaxillary and extends forward to the anterior end of that part of this bone that is preserved in the fossil. Whether it anastomosed at the anterior end of the snout with its fellow of the opposite side could not be determined.

The supratemporal canal arises from the main-infraorbital at the hind end of the supratemporo-intertemporo-extrascapular bone and there lies approximately dorsal to the latero-occipital process of its side of the head, this process being called by Stensiö the cranio-spinal. The canal anastomoses in the median line with its fellow of the opposite side to form a complete cross-commissure.

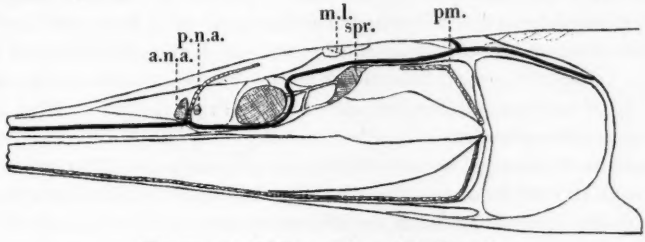

Fig. 21. *Saurichthys ornatus*. After Stensiö.

The supraorbital canal begins in the frontal at a point dorso-mesial to the orbital opening and from there, curving gradually antero-ventro-laterally, enters the so-called nasalo-antorbital and running downward between the two nasal apertures is said to anastomose by its anterior end with the main-infraorbital. It does not anastomose posteriorly with the main-infraorbital, its hind end lying a considerable distance antero-dorso-mesial to that part of the latter canal that traverses the dermo-sphenotic.

The preoperculo-mandibular canal begins in the dorsal limb of the preoperculum at a certain distance posterior to the hind edge of the spiracular opening and from there runs first posteriorly and then ventrally through the preoperculum to enter the mandible in which it turns forward and continues onward to the anterior end of that part of the mandible that is preserved in the fossil. There is no indication of either a jugal or an oralomandibular canal.

In *Saurichthys wimani* and *Saurichthys elongatus* Stensiö describes middle and posterior head lines of pit organs on each side of the head lying on the parietal, but in *Saurichthys ornatus* only the middle one of these two lines is described. In *Saurichthys wimani* there is no indication of a supratemporal cross-commissure, but it is shown well developed in *Saurichthys elongatus* and in the same position as in *Saurichthys ornatus*.

CONCLUSIONS

Comparing the conditions in the several craniates above considered, it seems quite certain that there were primarily in vertebrates three longitudinal latero-sensory lines on each side of the head and that they were crossed by more or less complete transverse intersegmental lines. The longitudinal lines were dorso-lateral, epibranchial and ventral in position, and the interbranchial portions of the intersegmental lines lay one along the antero-lateral edge of each of the visceral arches excepting only the premandibular. When the visceral clefts broke through, the related interbranchial lines were broken down and in large part if not entirely dispersed. In the hyal arch the related interbranchial line persisted as the preoperculo-mandibular (hyomandibular) in all the craniates considered excepting only the Petromyzontidae, while in the mandibular arch the dorsal portion of the related line persisted as the postorbital section of the main-infraorbital, the ventral portion of the line disappearing excepting possibly in the Petromyzontidae. In each of these two arches the related interbranchial line gives off a branch which runs anteriorly or antero-ventrally across the external surface of the next anterior arch and gives origin to the jugal-oralomandibular line and the suborbital and antorbital portions of the main-infraorbital.

The main-infraorbital line is probably not primarily a continuous line for if it develops in all vertebrates as described by Greil in *Ceratodus*, it is formed in relation to three primarily distinctly different sensory lines; a horizontal portion developed in relation to the epibranchial line, a descending postorbital portion developed in relation to a dorsal section of the branchial portion of the mandibulo-premandibular intersegmental line, and a suborbital and antorbital portion developed in relation to the antero-ventrally directed branch of the mandibulo-premandibular line, this line swinging upward into a horizontal position in connection with the incorporation in the chondrocranium of the dorsal half of the bar of the premandibular arch. The ethmoidal (internasal) anastomosis of the lines of opposite sides of the head and the recurrent anterior end of the line in many fishes are apparently in some way related to the bend in the premandibular bar between its dorsal and ventral portions. The antorbital section always passes ventral to the nasal capsule, but the anterior end of the suborbital section may be prolonged on to the dorsal surface of the nasal capsule as a supranasal loop, as in *Raia*, or there meet and anastomose with the anterior end of the supraorbital line, as in *Protopterus*. The otic section of the line, which forms the anterior end of the epibranchial portion, is thus not morphologically a part of the infraorbital portion of the line.

The supraorbital line is said by Platt to be, in *Necturus*, a direct anterior outgrowth of the primitive dorso-lateral sensory line, but in *Ceratodus* it is said by Greil to be a forward outgrowth of the epibranchial line. The anterior head line quite certainly develops in relation to the dorsal portion of the mandibulo-premandibular intersegmental line, and when it is present it usually anasto-

moses by its ventral end and never by its dorsal end with the supraorbital, which is favourable to Greil's view of the development of the supraorbital line. The supraorbital line, lying as it does anterior to the mandibulo-premandibular intersegmental line, must run forward across the external surface of the premandibular segment. When, in primitive vertebrates, it reached the anterior edge of that segment it apparently turned downward along that edge and, passing between the orbital opening and the nasal capsule, fell into the anterior end of the suborbital section of the main-infraorbital, this apparently being the condition in *Coccosteus*, *Perleidus*, *Cheirolepis* and *Birgeria*. Later, in connection with the development of cranial flexure, the supraorbital line bulged forward on to the dorsal surface of the nasal capsule and so gave origin to the supranasal loop of the Plagiostomi and the supranasal hook or simple line of *Macropetalichthys*, *Osteolepis*, *Polypterus* and most of the recent Teleostei. The supraorbital line always lies throughout its entire length dorsal or posterior to the nasal capsule, never, even when it has at its anterior end a recurrent course, passing ventral to that capsule. In the Osteostraci and Petromyzontidae it is accordingly either wholly wanting or represented by a short line that lies posterior to the single median nasal aperture.

The anterior, middle and posterior head lines are apparently related, respectively, to the mandibulo-premandibular, hyobranchial and first vagus intersegmental lines and are hence probably homologous in all craniates, but the supratemporal line varies so greatly in position in different fishes that it would seem as if it could not be developed in all of them in relation to the same intersegmental line.

The preopercular portion of the preoperculo-mandibular line is said to have been primarily connected with the main-infraorbital between its preauditory and postauditory portions, but the organs developed in relation to this line develop, in *Amia*, progressively upward and downward from a sensory patch that is wholly disconnected with the main-infraorbital. The canal, or groove, that may later develop in relation to this preopercular line may always remain wholly unconnected with the main-infraorbital, or it may acquire anastomosis either with the postorbital section of that canal, or with the horizontal section between its preauditory and postauditory portions. The first one of these two anastomoses occurs when the hyomandibula is of the plagiostomian or chondrostean type, the second anastomosis only when the hyomandibula is of the teleostean type. The preoperculo-mandibular line is more fully developed than the jugal-oralomandibular in those of the recent fishes considered in which the hyomandibula is of the teleostean type, the jugal-oralomandibular being the more fully developed one when the hyomandibula is of the selachian or batoidean type. In *Polyodon*, where the hyomandibula is of the chondrostean type, the preoperculo-mandibular line is the only one described, while in the Acipenseridae, where the hyomandibula is also of the chondrostean type, the jugal-oralomandibular line is the only one described.

In the fossil Rhipidistia, Palaeoniscidae and Saurichthydae the dorsal end

of the preopercular canal curves anteriorly and may be prolonged forward ventral to the spiracle, and associated with this the hyomandibula is apparently of the chondrostean type, while in the Catopteridae (*Perleidus*) the canal curves less markedly forward and the hyomandibula is apparently of the teleostean type. In *Wimania*, one of the Coelacanthidae, neither preopercular canal nor preopercular bone is described by Stensiö, and a hyomandibula developed from the branchial rays of the hyal arch is apparently in process of formation but not yet functional (Allis, 1928). In the Arthrodira the preopercular canal anastomoses by its dorsal end with the main-infraorbital between its preauditory and postauditory portions, but it is exceedingly improbable that the hyomandibula of these Fishes, if it was present, was of the teleostean type. What has apparently taken place is that the preopercular sensory patch, in shifting ventrally as it does in early embryos of *Amia*, pulled the epibranchial portion of the main-infraorbital after it and so retained its primitive connection with that line, instead of becoming detached from the latter line and then growing upward to acquire secondary attachment with it in connection with the development of a teleostean hyomandibula.

There are thus certain features in the distribution of the latero-sensory lines that are in large measure characteristic of each of the large groups or orders of the craniates above considered, but there is nothing that seems to definitely indicate lines of descent. It is, however, to be noted that the latero-sensory lines may present two markedly different patterns of distribution in the two large subdivisions of most of these large groups or orders: as in the Osteostraci and Heterostraci, which are the two large subdivisions of the Ostracodermi; in the Macropetalichthyids and the non-Macropetalichthyids, which are the two large subdivisions of the Arthrodira; in the Ceratodontidae and Lepidosirenae, which are the two large subdivisions of the Dipnoi; in the Plagiostomi and Holocephali, which are the two large subdivisions of the Elasmobranchii; and in the Saurichthydae and non-Saurichthydae, which are the two large subdivisions of the fossil Chondrostei. In so far as the latero-sensory lines alone are concerned, the conditions in *Macropetalichthys* would seem to lead through *Osteolepis* and *Polypterus* to *Conger* and certain of the Teleostei, the conditions in *Coccosteus* leading to the fossil Chondrostei and there separating into two lines, one leading to the recent Chondrostei and the other to the Holostei.

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EXPLANATION OF LETTERING

■	Main-infraorbital and supratemporal lines or canals.
▥	Supraorbital line or canal.
▨	Preoperculo-mandibular, jugal-oralo-mandibular and head lines or canals.
a.l.	Anterior head line.
a.n.a.	Anterior nasal aperture.
cb.	Circumbuccal line.
dl.l.	Dorso-lateral line.
end.	Opening of the endolymphatic duct.
ep.l.	Epibranchial line.
eth.	Ethmoidal canal or line.
eye	Orbital opening.
g.l.	Gular line.
h.c.l.	Horizontal cheek line (jugal).
hm.	Hyomandibular line or canal.
in.a.	Internasal anastomosis.
io.	Main-infraorbital line or canal.
it.a.	Internasal anastomosis.
jg.	Jugal line or canal.
j.m.	Jugal-oralomandibular line or canal.
m.c.l.	Mandibular cheek line.
m.l.	Middle head line.
n.a.	Single nasal aperture.
omd.	Oralomandibular line or canal.
p.l.	Posterior head line.
pm.	Preoperculo-mandibular line or canal.
p.n.a.	Posterior nasal aperture.
spr.	Spiracular opening.
so.	Supraorbital line or canal.
st.	Supratemporal line or canal.
v.c.l.	Vertical cheek line.
v.l.	Ventral longitudinal line.

ANATOMICAL NOTES

ON THE OCCIPITO-ATLANTO-AXIAL ARTICULATIONS

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THIS note is intended to direct attention to certain minor and generally neglected details in the descriptive anatomy of the occipito-atlantal and atlanto-axial joints, details usually omitted from current text-books, yet not devoid of interest and importance. These details are the outcome of a recent examination of much human and comparative autopsy material checked against the investigation of dry skeletal preparations. The human material consisted of an age-series[1] of 85 cervical columns excised entire and studied by section or dissection. The comparative material was obtained from the Zoological Society's Prosectorium and elsewhere, its range being indicated by Table I. The Museum of the Royal College of Surgeons provided the osteological preparations listed in Table II. Attention is more particularly drawn to the precise attachment of capsular and other ligaments and to a commonly ignored feature of these articulations—the constancy of intracapsular retro-synovial fatty pads or fringes, which discharge here the same physiological rôle they perform in the majority of diarthroses elsewhere in the body, and of whose apparatus they constitute indeed a necessary mechanical part.

A. *The atlantal lateral mass*

As a detailed survey of the atlantal lateral mass must necessarily disclose much of the intimate anatomy of the occipito-atlanto-axial articulations, it is somewhat surprising that this structure should fail to be accorded in our modern authoritative treatises the attention it merits. Doubtless in an attempted simplification of matters for the student's benefit, current text-books concern themselves principally with the shape and disposition of articular processes, and with simple accounts of the attachments of the capsular and transverse ligaments. Nowhere is a complete description of the lateral mass available; even Frazer's (3) account, more elaborately detailed than most, being deficient in some respects. This present-day lack of detailed text-book information stands in marked contrast with the high standard of accurate observation and painstaking record established by the older British anatomists, such as Humphry (4) and Morris (6), whose extraordinarily excellent records leave but small room for additional comment. Indeed, the observations independently submitted here (in the hope of remedying existing text-book deficiencies) constitute very largely a mere confirmation of their findings, as well as a tribute to their skill and accuracy.

The bony pillar of the lateral mass is of hour-glass appearance in sagittal section and almost triangular in coronal section. This triangular appearance is due to the strong medial convergence of the planes of the articular surfaces; the apex of the "triangle" is, however, replaced by the medial surface of the mass, which assists the remaining lateral, superior and inferior surfaces in the circumscription of the bone. The lateral surface which is about 1 in. high and forms the base of the "triangle" is convex save where smoothed by the impress of the vertebral artery. It bears ventrally the anterior (costal) tubercle, laterally, the transverse process complex, and dorsally, where it overhangs the neural arch, a strong prominent tubercle (*tuberculum superius atlantis*). It will be readily appreciated that the atlas vertebra bears typically no less

[1] Made up as follows: From birth to 1 year old, 34 spines; from 1 to 10 years, 23; from 10 to 20 years, 20; from 20 to 30 years, 8; total, 85 spines.

than seven tubercles all meriting descriptive recognition. These are (1) the *tuberculum anterius* of the anterior arch, (2) the *tuberculum posterius vel spinosum* of the posterior arch, (3) the almost obsolete anterior tubercle (*tuberculum costalis anterius*) borne upon the front of the lateral mass and connected by the pre-arterial crus of the so-called transverse process, with (4) the posterior tubercle (*tuberculum costalis posterius*) which includes the whole of the tip of the descriptive transverse process whatever its degree of pseudo-bifidity. These four tubercles are usually accorded recognition, though their correct morphological significance is not always appreciated. Next is (5) the superior or post-foveolar tubercle (*tuberculum superius atlantis*), the strong rough prominence upon the dorsal aspect of the lateral mass close to its upper limit and immediately behind the dorsal extremity of the superior articular process; it is often connected by bone to the dorsal lip of the *sulcus arteriae vertebralis*; (6) is the well-recognised *tuberculum ligamenti transversi atlantis*, and (7), when well developed, is the tiny tubercle (*tuberculum ligamenti accessorii*) which lies immediately behind (6) and serves for the attachment of the accessory axio-atlantal fibres.

Skirting the lateral and posterior aspects of the periphery of the superior articular process and extending for its whole length is a deeply incised groove (*sulcus cap-*

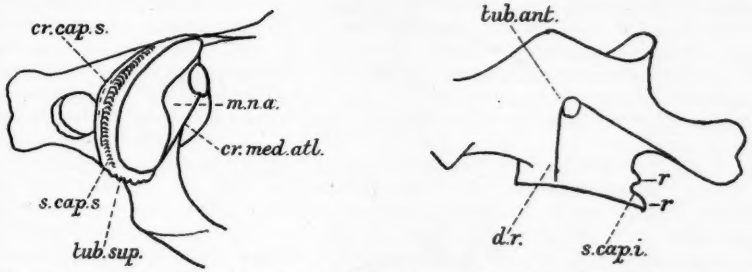

Fig. 1. Superior and anterior aspects of the lateral mass. The left-hand figure shows superior atlantal tubercle (*tub.sup.*), superior capsular sulcus (*s.cap.s.*), and crest (*cr.cap.s.*), medial atlantal crest (*cr.med.atl.*) and medial non-articular area (*m.n.a.*). The right-hand figure shows the inferior capsular sulcus (*s.cap.i.*) with its limiting ridges (*r*, *r*), and the anterior costal tubercle (*tub.ant.*) with the ridge (*d.r.*) descending therefrom.

sularis superior), deepest opposite the vertebrarterial foramen and itself bounded laterally, especially in its dorsal half or so, by a rough raised lip (*crista capsularis superior*). This rough lip serves for the attachment of the occipito-atlantal capsule and its strengthening bands (see fig. 1). The lower portion of the convexity of the lateral mass exhibits further ligamentous markings, those of the atlanto-axial capsule. These take the form of a definite linear groove (*sulcus capsularis inferior*) bounded above and below by two quite obvious lips whereof the upper is usually the more pronounced. The groove starts from the antero-internal edge of the inferior articular process, sweeps successively around the anterior, lateral and posterior aspects of the mass to terminate on the medial surface thereof close to its origin or on the caudal aspect of the tubercle for the transverse atlantal ligament. An appreciable segment of the lower end of the lateral mass is therefore intracapsular.

The superior surface of the mass presents three distinct areas—a middle articular area (the *fovea articularis superior* itself) separating lateral from medial non-articular regions. The concavity of the fovea is most marked antero-posteriorly; its floor slopes abruptly latero-medially, thereby greatly abbreviating the depth of the medial surface of the mass, and though of typical outline exhibits a marked tendency towards subdivision. Macalister (5) regarded the upper articular area as formed by "two confluent facets." Inspection of some 200 atlas vertebrae showed its outline to be

reniform in 50 per cent. cases owing to the medial indentation about its middle (caused by the encroachment of the medial non-articular area): to be of hour-glass appearance in 20 per cent. cases due to an additional lateral indentation: and of still more pronounced hour-glass outline in a further 25 per cent. cases owing to an incomplete junction of these two indentations, an abortive attempt, as it were, to form a transverse transarticular groove: in the remaining 5 per cent. or so of specimens the transarticular groove was fully established, the articular area comprising two distinct and discontinuous facets.

The lateral non-articular area lies between the fovea articularis and the roots of the transverse process; it bears the *sulcus capsularis superior* with its limiting *crista capsularis superior*. The medial non-articular area lies between the fovea and the medial surface of the mass itself. Approximately triangular in outline, it is limited above by the indented medial edge of the fovea, antero-inferiorly by the *tuberculum ligamenti transversi* (either solely, as when the tubercle attains to the foveal border, or additionally, as when the tubercle is small, and falls short thereof, by the ridge (*crista supratubercularis*) connecting this eminence with the antero-medial margin of the articular area) and postero-inferiorly by the *crista medialis atlantis*, i.e. the con-

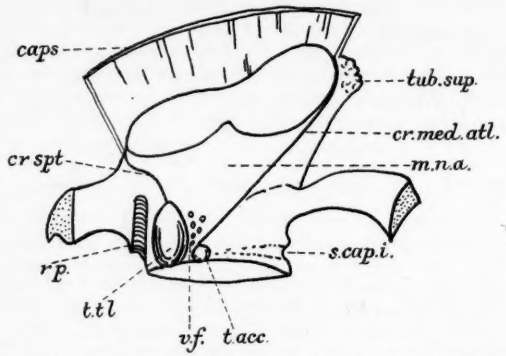

Fig. 2. Medial aspect (diagrammatic) of half atlas showing superior atlantal tubercle (*tub.sup.*), medial atlantal crest (*cr.med.atl.*), medial non-articular area (*m.n.a.*) with its vascular foramina (*v.f.*), the transverse (*t.t.l.*) and accessory (*t.acc.*) tubercles, the pretubercular recess (*r.p.*) and the supratubercular crest (*cr.spt.*).

stant, prominent ridge running from the region of the superior atlantal tubercle (defined above) to the caudal aspect of the tubercle for the transverse ligament. This last tubercle, with its supratubercular crest, forms the anterior and minor portion, whilst the medial atlantal crest forms the posterior and major portion, of the boundary between the superior and medial surfaces of the lateral mass. The rough excavated floor of the non-articular area is wholly within the occipito-atlantal capsule, whose attachment is to the periphery of this area and not, as is so often stated, to that of the upper articular process. The excavation is constantly occupied by a pad of retro-synovial fatty tissue, varying in actual size with the degree of subdivision of the articular area. This fatty pad is typical of the mammalian occipito-atlantal joint (*vide infra*) and in Man was first noted by Morris, who, very aptly, gave its magnitude as the "size of a split pea." Immediately behind the *tuberculum ligamenti transversi* (as noted by Macalister and Frazer) numerous vascular foramina pierce the floor, disposed either row-wise alongside the tubercle or congregated into a little vascular pit which sometimes interrupts the junction of the medial atlantal crest with the tubercle. Here the capsular ligament is weak or actually so deficient that, besides the

vessels, the lining synovial membrane escapes and establishes continuity with the synovial sacs about the odontoid process.

The medial surface of the lateral mass is its smallest. Its main feature, the oval, bead-like tubercle for the transverse ligament, separates a brief anterior from a more extensive posterior portion. The anterior part is taken up by the *recessus pretuberculari*s, a narrow vertical cleft, close to the origin of the anterior arch, for the reception of ligamentous odontoid fibres and with a floor pitted by vascular foramina. The post-tubercular area is roughly triangular with its apex at the tubercle. It is bounded by the medial atlantal crest superiorly, by the medial edge of the inferior articular process inferiorly, and by the dorsal border of the lateral mass posteriorly. Its depth varies on the average from $\frac{1}{8}$ in. near the tubercle to some $\frac{7}{8}$ in. at its maximum posteriorly. Close behind the major tubercle and below the termination of the medial crest is the (occasional) tubercle for the accessory axio-atlantal ligament, a tiny knob visible also from the under aspect of the bone, where it encroaches upon and affects the outline of the inferior articular process. Curving inwards from the lateral aspect of the mass to join this little tubercle, and running very close to the lower articular margin, is the *sulcus capsularis inferior*, here much less well marked than elsewhere. The medial crest, about half-way along its length, gives origin to and is strengthened by the internal (spinal) edge of the posterior arch. Above this origin the medial surface is in close relationship with the vertebral artery and below it with the extradural fat. (Though not recognising this medial surface as an entity Macalister nevertheless noted an "internal tuberosity" on the atlas, which he divided, by the passage of the nutrient vessels, into anterior and posterior parts, the former giving attachment to the transverse ligament.)

The inferior surface of the lateral mass is the *facies articularis inferior*, concave in the dried bone but definitely convex in the fresh state owing to its incrustation of cartilage which may attain an adult maximum thickness of over 1·5 mm. Though commonly of a characteristic oval figure the outline of this facet at times defies easy geometrical description, its curvature being interrupted by the caudal prolongation of the accessory tubercle and by anterior and medial flattenings in the plane of the corresponding surfaces of the mass, and largely due to their inferior prolongation. When pronounced the anterior flattening extends from the junction of the facet with the anterior arch medially to the plane of the anterior tubercle laterally, and is there terminated by a ridge (see fig. 1) descending from that tubercle. The medial flattening extends from the anterior arch region to its dorsal termination by the accessory tubercle. Occasionally a more indefinite lateral flattening is present, tending to reduce the contour of this surface to that of an irregular pentagonal curvilinear figure.

B. *Ligamentous attachments*

The anatomy of the cervico-cranial ligaments has been so exhaustively treated in the past that little remains for fruitful comment. Present findings mostly confirm old and well established observations. The considerable synonymy which has accumulated around these structures (due partly to their considerable individual variation) has been listed by Fick (2). Among British authorities Quain (7) alone follows the Continental description of the membrana tectoria by recognising therein superficial and deep (median and lateral) portions. Whilst formalin preservation does not facilitate, and practical considerations do not perhaps enforce this subdivision, yet it might be retained in the interests of both fact and British anatomical history, since the deep median structure was Humphry's cervico-basilar ligament, Morris's occipito-cervical, and Macalister's *ligamentum latum axiale*. Distinct lateral portions of this layer are occasionally obvious (or can be so rendered by a little dissection) forming postero-medial supports for the occipito-atlantal capsules. The accessory axio-atlantal ligaments lie rather deep to these lateral portions and appear not to belong thereto

but to the cruciate system. The occipito-atlantal capsule has its inferior attachment well outside the periphery of the superior articular process. On the ventral face of the lateral mass it descends some 2 or 3 mm. below the cranial edge of the bone, from which it sweeps infero-laterally to the upper aspect of the root of the anterior limb of the transverse process; thence it passes postero-superiorly above the vertebrarterial foramen to reach the superior atlantal tubercle on the back of the mass. From this tubercle the capsule descends infero-medially along the medial atlantal crest to gain the tubercle for the transverse ligament beyond which it has attachment to the *crista supratubercularis* and thereby reaches the anterior arch region again. A cranial cuff of the lateral mass as well as the whole of the medial non-articular area is therefore intracapsular. Constant thickenings of the capsule occur. A lateral or anterior oblique ligament (*lig. occ.-atl. ant. obl.*) consists of fibres radiating upwards and forwards from the base of the transverse process. A stout bundle (*lig. occ.-atl. post. obl.*) extends upwards and inwards from the superior atlantal tubercle and is often continuous with the fibrous arch over the vertebral artery. Medially, in the region of the transverse ligament's tubercle, the capsular fibres are thin, weak and often deficient, permitting egress of the synovial membrane. In some specimens the capsule proper is here hard to identify, being masked by the supporting contributions from stronger neighbouring ligaments, e.g. the transverse, lateral odontoid and accessory axio-atlantal ligaments, together with the strong odonto-atlantal fibres (*vide infra*) and the deep lateral portion of the membrana tectoria.

The atlanto-axial capsule is also attached beyond the limits of the articulating surfaces of the contiguous vertebrae, as figured by Testut (8). Its atlantal attachment has already been considered under its markings upon the lateral mass where it does not attain so closely to the transverse process as Testut's diagram would imply. On the axis, in the spinal and odontoid regions, it follows pretty closely the margin of the articular facet, but from the odontoid ventrally it rapidly descends some 2 or 3 mm. in passing to the transverse process. There it grooves both limbs of the process, skirts the medial side of the vertebrarterial foramen and reaches the neural arch 2 or 3 mm. behind the dorsal limit of the cartilage. The vertebral artery laterally, and the second spinal nerve posteriorly, are most intimate relations, the nerve having closer contact with the capsule than with the neural arch.

The transverse ligament has the cranial aspect of its lateral extremities smoothed by the prolongation of the posterior odontoid bursa. It is attached to its appropriate tubercle and to the occipito-atlantal capsule as stated previously. A superior crus to the cruciate apparatus can usually be found, but the inferior crus is not always present. The degree of development of the inferior crus seems to vary inversely with that of the accessory axio-atlantal ligaments, suggesting that these latter belong to the cruciate system rather than to the membrana tectoria. The accessory ligament arises from a roughness (frequently a vertically disposed tubercle or tiny crest) on the upper spinal aspect of the axis body. It passes obliquely to its insertion, directly behind that of the transverse ligament, partly into the accessory tubercle and partly into the occipito-atlantal capsule. The density of the ligaments and the presence of much fat-laden areolar tissue render dissection about the odontoid process somewhat difficult. The median odontoid (suspensory) ligament may be quite easily destroyed before being recognised, or aberrant bundles of weak fibres mistaken for other structures. The lateral odontoid (alar, check) ligaments are substantial bands often completely clothing the back of the odontoid head, and supporting laterally by their extremities the capsules of the occipito-atlantal joints. Their uppermost fibres may be continuous across the middle line forming the "faisceau occipito-occipital" of French authors. On a slightly anterior plane to these, but belonging to the same system, are the constant dense odonto-atlantal fibres, bundles which extend from the dens to the pretubercular recess on the atlas and which serve to separate the anterior from the posterior odontoid synovial sac.

C. *Synovial membranes*

The synovial linings of the occipito-atlanto-axial articulations clothe the non-articular intracapsular areas already indicated, and are inflected as fringes containing retro-synovial fat. Their extensive cavities manifest a marked faculty for intercommunication, doubtless in response to functional needs, but also reminiscent of their evolutionary history, since the five Mammalian diarthroses are derived from the single primitive Reptilian enarthrosis. Of this ancestral joint cavity the anterior odontoid sac, mostly well circumscribed, may represent an isolated part, the more extensive posterior sac being bursal in nature and communicating freely with either the occipito-atlantal joint (above and behind the transverse ligament's attachment) or the atlanto-axial joint (on its antero-medial aspect) or even with both joints. It has not been possible to confirm Cunningham's (1) observation on the continuity of these two sacs, which, however, any deficiency in the odonto-atlantal fibres must facilitate.

D. *Intracapsular synovial fringes*

Owing to the incongruity of opposing surfaces retro-synovial fat is present in the occipito-atlantal and atlanto-axial joints. The synovial membrane is infolded in a more or less circumferential manner, best illustrated in the latter joint, particularly on its antero-lateral and postero-medial aspects, where the synovial fringe may extend inwards over the cartilage for a distance of about 4 mm. The occipito-atlantal articulation shows a constant fatty pad in contact with the medial non-articular area described. Its size varies chiefly with the extent of that area, and with the degree of subdivision of the upper atlantal facet, but is subject also to slight individual variation. Frequently a smaller pad occurs in the region of the lateral indentation of the facet, and occasionally a tiny posterior pad is also present. Not uncommonly a well-marked fatty fringe occupies the whole length of the internal aspect of the medial part of the capsule.

E. *Comparative anatomy*

To determine whether or not these intracapsular structures were peculiar to Man on account of his specific posture, the fresh material listed in Table I (*q.v.*) was examined for their presence, and the wider range of dried preparations shown in Table II for inferential evidence of their occurrence in the shape of a medial non-articular atlantal area. It was found that the occipito-atlanto-axial complex retains its essential structure throughout the Mammalian series, with the exception of the Prototheria and of such highly modified Eutherian forms as the Cetacea and Sirenia. Minor modifications, of ordinal or of specific value, reflect the functional demands made upon this apparatus (and the whole cervical spine) by posture, diet, mode of life, methods of defence or attack, and the peculiarities of cranial structure. Thus the typical carnivorous type is characterised by excellent congruity of occipital condyle with undivided atlantal fovea and by very small intracapsular fringes. The contrasting ungulate type shows less congruity of divided condyle with partially or completely divided atlantal fovea and large intracapsular fringes or pads. The primate type, with its own peculiarities, enjoys a moderate degree of congruity and shows correspondingly moderately developed pads (see Table I). Despite these generalities, the fatty pads were relatively large in *Papio hamadryas* among Primates, the Agouti (*Dasyprocta aguti*) among Rodents, and in the Gray Seal (*Halichoerus grypus*), Coati (*Nasua rufa*), Sun Bear (*Ursus malayanus*), and Leopard Cat (*Felis bengalensis*) among the Carnivora. Individual variation was manifested in the cases of the Panda (*Aelurus fulgens*), Binturong (*Arctictis binturong*), Genet (*Genetta rubiginosa*), and Persian Gazelle (*Gazella subgutturosa*). One specimen of Bush-baby (*Galago*) exhibited all three pads as described in the human subject. It is evident therefore that these structures form an essential part of the cervico-cranial articular apparatus and are uniformly distributed throughout the Mammalia.

Summary

1. The descriptive anatomy of the occipito-atlanto-axial articular apparatus of Man is reviewed and somewhat amplified.

2. Retro-synovial fatty pads or fringes in these joints are not peculiar to Man but occur in the majority of Mammals.

Table I. ***List of Mammalian species examined for presence of occipito-atlantal intracapsular fatty pads.***

PROTOTHERIA. (No material.)

METATHERIA. (Pads relatively small.)
Macropus giganteus, M. rufus, Phascolomys tasmaniensis.

EUTHERIA.

(1) Ungulata (pads large, often huge).
Sus scrofa, Camelus bactrianus, Cervus elephas, C. dama, C. canadensis, C. eldi, Rangifer tarandus, Odocoileus virginianus, Cephalophus dorsalis, Cobus leche, Antilope cervicapra, Gazella subgutturosa, Ourebia nigricaudata, Capra hirca, C. aegagrus, Ovis aries, O. musimon, Ammotragus levia, Haplocerus montanus, Bos taurus, B. grunniens, B. indicus, Bubalus buffelis, Bison americanus, Equus caballus.

(2) Rodentia (pads relatively small).
Callosciurus Prevostii, Petaurista petaurista, Marmota monax, Vizcacia viscacia, Dasyprocta aguti, Dolichotis salincola.

(3) Carnivora (pads small to tiny; rarely large).
Felis tigris, F. caracal, F. rufa, F. bengalensis, F. tigrina, Cynaelurus jubata, Viverricula malaccensis, Civectis civetta, Genetta rubiginosa, Paradoxurus hermaphroditus, P. larvatus, Arctictis binturong, Herpestes spec., Crossarchus obscurus, Canis familiaris, C. lupus, C. adustus, Otocyon megalotis, Pseudolopex griseus, Ursus malayanus, Aelurus fulgens, Nasua rufa, Cercoleptes caudivolvulus, Mustela martes, Halichoerus grypus.

(4) Primates (pads small to moderate).
Galago garnetti, Lemur macaco, Lagothrix Humboldtii, Cebus fatuellus, C. apella, Ateles paniscus, Macacus rhesus, M. cynomolgus, Presbytes entellus, Cynopithecus niger, Cercopithecus sabaeus, C. tantalus, Semnopithecus entellus, Theropithecus gelada, Papio hamadryas, P. cynocephalus, Simia satyrus.

Table II. ***List of Mammals examined for presence of an atlantal medial non-articular area. This area is not evident in Cetacea and Sirenia. Numerals indicate number of specimens examined.***

PROTOTHERIA.
Ornithorhynchus anatinus (4), *Echidna aculeata* (3).

METATHERIA.
Didelphys virginiana (2), *D. azarae, D. cancrivora, Thylacinus cynocephalus* (3), *Dasyurus ursinus, Perameles lagotis, Phascolomys wombat* (2), *Phascolarctus cinereus* (2), *Aepyprymus rufescens, Macropus rufus* (2), *M. ruficollis* (3).

EUTHERIA.

(1) Edentata.
Bradypus torquatus, Choloepus didactylus, Myrmecophaga jubata, Tamandua tetradactyla, Dasypus villosus, Orycteropus capensis.

(2) Sirenia.
Manatus, Halichore dugong (2).

(3) Cetacea.
Platanista gangetica, Phocoena communis (2), *Delphinus tursiops* (3), *D. delphis* (2).

Table II (*continued*).

EUTHERIA (*continued*).

(4) Ungulata.
Hippopotamus amphibius, Sus scrofa (4), *Auchenia glama, Tragulus spec., T. napu* (3), *Dorcatherium aquaticum, Cervus dama, C. davidianus, C. elaphus* (3), *Rangifer tarandus, Alces machlis, Cariacus mexicanus, Okapia johnstoni, Alcelaphus tora, Connochoetes taurina, Antilope cervicapra, Gazella levipes, Boselaphus tragocamelus* (3), *Capra ibex, C. rupicapra* (2), *C. hirca* (3), *Haplocerus montanus, Ovis aries* (2), *Bos indicus, Bubalus buffelis, Bison bonasus.*
Tapirus indicus, T. americanus, Equus caballus (2).
Hyrax (*Procavia*) *capensis. Elephas indicus.*

(5) Rodentia.
Capromys pilorides, Castor canadensis (4), *Syntheres mexicanus, Hystrix cristata, H. javanica, H. hirsutirostris, Dasyprocta aguti, Coelogenys paca* (2), *Cavia porcellus* (3), *Hydrochoerus capybara, Lepus campestris, L. cuniculus* (2).

(6) Carnivora.
Felis tigris (2), *F. pardus* (3), *Canis familiaris* (6), *C. vulpes, C. lagopus* (3), *C. bengalensis, Nyctereutes procyonides, Otocyon megalotis, Ursus spelaeus, U. americanus, U. maritimus* (2), *U. tibetanus, Melursus ursinus* (2), *Procyon lotor* (2), *P. cancrivorus, Bassaris astuta* (2), *Nasua rufa* (2), *N. narica, Cercoleptes caudivolvulus* (4), *Lutra vulgaris* (3), *Meles taxus* (3), *Mellivora indica* (2), *Galictis vittata, Mustela putorius* (4), *M. furo* (2), *Gulo luscus* (2), *Otaria jubata, O. australis, Phoca vitulina, Monachus albiventer.*

(7) Insectivora.
Erinaceus europaeus.

(8) Chiroptera.
Pteropus rubricollis, P. vampyrus, Vampyrus lineatus.

(9) Primates.
Brachyteles arachnoides, Semnopithecus schistaceus, Theropithecus gelada, Papio anubis, P. porcarius, P. hamadryas, P. babuin, Simia satyrus (6), *Gorilla gorilla* (3), *Anthropopithecus troglodytes* (4).

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RIGHT STERNALIS MUSCLE WITH EXPANDED FENESTRATED TENDON

By Prof. C. J. PATTEN

Sex: male. Age: sixty-five. Condition: muscular

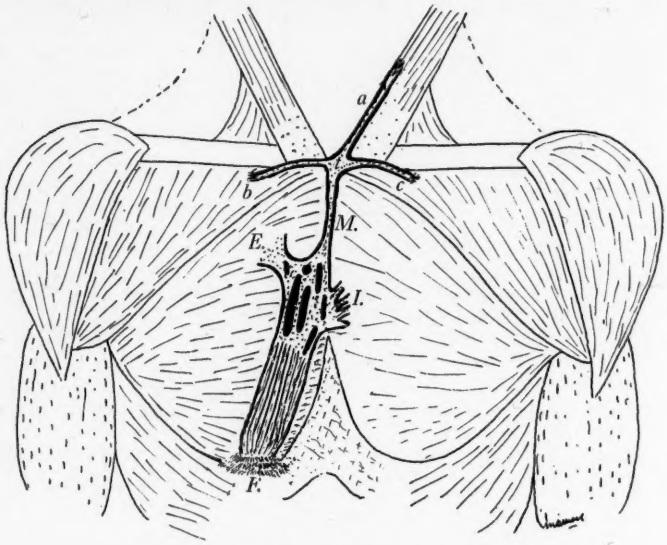
The upper attachments of this sternalis muscle were represented by three heads.

(1) External: short, thin, expanded, and fibrous; differentiated from that part of the deep fascia of the right pectoralis major related to the inner end of the fourth rib.

(2) Middle: divisible above into three slips as follows:

(*a*) A long, thin, cord-like tendon continuous on the medial side of the lower third of the left sterno-mastoid muscle to its origin.

(*b*) A thin, cord-like tendon directed horizontally and mesially from the inner fibres of the clavicular head of the pectoralis major of the right side.



Sketch of sternalis muscle (semi-diagrammatic).

E. external head; short, and expanded. *M.* middle head; long and narrow. *a, b, c,* slips of origin of middle head, blending in a triangular small expansion (*t*). *I.* inner head; short, tendinous strands. *F.* fascial attachment below fleshy fibres, short and expanded.

(*c*) A tendon, similar in character—though slightly smaller—and directed in a corresponding manner from the inner fibres of the clavicular head of the pectoralis major of the left side.

These three slips united in the middle line between the origins of the sternal heads of either sterno-mastoid muscle. They gave rise to a small triangular expansion, from which a single narrow, long tendon descended in the middle line to the level of the third intercostal spaces.

(3) Internal: several strands of tendinous fibres springing from the sternum, and inner edge of the costo-sternal origin of that part of the left pectoralis major opposite to the level of the fourth and fifth ribs.

The three heads fused, each contributing to the formation of an expanded fenestrated thickened membrane, or flattened tendon, which stood out in bold relief from the deep fascia clothing the surrounding area of the right pectoralis major muscle. The fenestrated tendon extended from the upper border of the inner end of the fourth right costal cartilage to the lower border of the inner end of the fifth right costal cartilage. Continuous with this tendon a flat, strap-shaped muscle descended with a slight degree of obliquity to the right. This part of the sternalis muscle was composed in the main of fleshy fibres, which were directed longitudinally, i.e. in the long axis of the muscle, exhibiting a striated appearance. The fleshy fibres terminated below in a short fascial expansion which blended with the deep fasciae investing the inferior border of the right pectoralis major and the upper limits of the right rectus abdominis muscles. It should be noted that a considerable part of the costo-sternal origin of the right pectoralis major lies to the medial side of, and is uncovered by, the whole length of the fleshy segment of the sternalis muscle.

Although this sternalis derived slips of origin from the left pectoralis major and left sterno-mastoid muscles, the left sternalis itself was completely absent.

Dimensions

Fenestrated expansion	4 cm.
Slip (*a*) of middle head, to triangular expansion	7·4 cm.
Muscular part, length	6 cm.
Muscular part, maximum width (3 mm. narrower above and below) ...	2 cm.
Fascial insertion, length	1·9 cm.
Lowest point of medial border from mid-line (of sternalis muscle) ...	2 cm.

Nerve supply

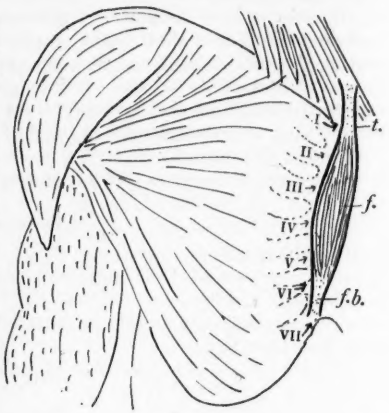
Small terminal twigs of the anterior branches of the 4th and 5th right intercostal nerves made their way through the fenestrated expansion, and thence to the skin, while the fleshy part of the muscle received twigs from the right external anterior thoracic nerve.

RIGHT STERNALIS MUSCLE, NARROW AND SPINDLE-SHAPED

By Prof. C. J. PATTEN

Sex: male. Age: sixty. Condition: muscular

The upper end of this sternalis muscle took the form of a single, stout, cord-like tendon. It blended intimately with the inner edge of the flattened tendinous origin of the sternal head of the right sterno-mastoid muscle. It showed no direct attachment to the clavicle. At the level of the inner end of the first right intercostal space its place was taken by fleshy fibres which were continued downwards to the level of the inner ends of the sixth and seventh right costal cartilages. Here the fleshy fibres were represented by a narrow fibro-fascial band. This blended with that part of the deep fascia which clothed the attachments of the right pectoralis major to the inner ends of the sixth and seventh right costal cartilages. (In this subject the greater pectoral muscles of either side derived slips of origin from the inner extremities of the seventh costal cartilages.) This sternalis was well developed, fusiform in contour, albeit narrow and attenuated. It was, for the most part, composed of fleshy fibres, vertically directed. A series of definite, fleshy slips were attached to the right pectoralis major at points corresponding to the costal slips of origin of the latter muscle—one to five inclusive. The inner edge of the right pectoralis major was completely occluded from view by the overlying sternalis, which, conformably with its fleshy fibres, ran downwards in a markedly vertical direction, skirting the right edge of the sternum and tips of the upper seven costal cartilages. The left sternalis was absent.



Sketch of sternalis muscle (semi-diagrammatic).

I to VII, arrows indicate the costal origins of right pectoralis major and sternalis. Arrows I, VI, VII are thickened to indicate strong attachments of sternalis. *t.* stout, cord-like tendon. *f.* fleshy fibres. *f.b.* fibro-fascial band.

Dimensions

Total length	11 cm.
Maximum width (level of third costal cartilage) ...	1·5 cm.
Width (level of lower border of clavicle)	0·6 cm.
Width (level of seventh costal cartilage)	0·9 cm.

N.B. Muscle tendinous down to 5 cm. below upper attachment. Muscle fibro-fascial up to 3 cm. above lower attachment.

Nerve supply

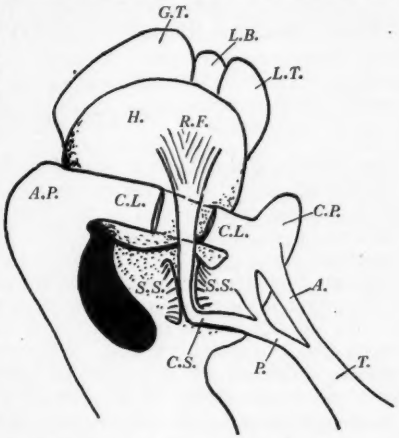
Several fine twigs derived from the external anterior thoracic nerve entered the deep surface of the muscle after they had pierced the lower part of the inner region of the right pectoralis major muscle.

BILATERAL CAPSULAR INSERTION OF PART OF THE TENDON OF THE PECTORALIS MINOR

By Prof. C. J. PATTEN

Sex: male. Age: forty-three. Condition: exceptionally muscular

Each pectoralis minor muscle exhibited the usual origin and relations, and in each the form and other details of the tendon and the manner in which part of it was inserted into the capsule of the shoulder-joint was practically identical. Hence, it is only necessary to describe the variation of one side. About 2 cm. below the coracoid process the tendon of the pectoralis minor —longer and more narrow than normal— split into an anterior and a posterior slip. They converged on reaching the coracoid process, on to which, taken together, they were inserted along the normal line of attachment. The interval between the slips was bridged over by loose fascia; this was pierced by a small artery—a branch from the thoracic axis. From the posterior slip, midway between its commencement and termination, a rounded tendon branched off which swept across the upper and dorsal aspects of the base of the coracoid process. It next altered its course by turning at a right angle, whence it proceeded forwards and downwards towards the shoulder-joint. It passed *en route* deep to the coraco-acromial ligament, free of any attachment, until it reached the capsule of the joint with which its fibres blended. Here the tendinous insertion reinforced the capsule, and its radiating fibres were comparable to those of the coraco-humeral ligament. Such an accession of capsular fibres was traceable anteriorly to the position of the subjacent tendinous long head of the biceps. This capsular tendon of the pectoralis minor, for the greater part of its length, was invested by a synovial sheath, prolonged backwards so as to intervene between the tendon and the base of the coracoid process. The synovial sac seems to have been an independent structure, which had no communication with the synovial lining of the cavity of the shoulder-joint.



Sketch of capsular insertion of part of the pectoralis minor (semi-diagrammatic). Left side from above.

T. tendon of pectoralis minor; longer and narrower than usual. *A.* anterior slip of tendon. *P.* posterior slip of tendon. *C.S.* capsular slip of tendon. *S.S.* synovial sheath (opened). *C.L.* coraco-acromial ligament (part cut away). *R.F.* radiating fibres of capsular tendon blending with coraco-humeral ligament. *H.* head of humerus enclosed in capsule. *G.T.* greater tuberosity of humerus. *L.T.* lesser tuberosity of humerus. *L.B.* long head of biceps. *C.P.* coracoid process. *A.P.* acromial process.

This aberrant tendinous slip of the pectoralis minor, on both sides of the body, passed deep to the coraco-acromial ligament on its way to the capsule of the shoulder-joint. A synovial sac intervened between tendon and ligament. There were no indications that the tendon or even part of its fibres pierced the coraco-acromial ligament.

I am greatly indebted to Dr MacConaill for the three line-drawings.

A NOTE ON THE SUPERIOR PETROSAL SINUS AND ITS RELATION TO THE SENSORY ROOT OF THE TRIGEMINAL NERVE

By A. E. COATES
Anatomy Department, Melbourne

The relation of the superior petrosal sinus to the sensory root of the fifth nerve is indifferently described in current text-books of anatomy. Most authors figure the sinus passing over the root at the superior margin of the petrous portion of the temporal bone. Fraser (*Anatomy of the human skeleton*), Poirier (*Traité d'anatomie humaine*), Gray's *Anatomy*, Morris's *Anatomy*, Quain's *Anatomy*, and Spalteholz's *Atlas* all show the sinus passing over the root of the trigeminal nerve. Piersol makes no mention of the relation. Cunningham figures the sinus beneath the root.

An investigation of this region was undertaken in the Dissecting Room at the Melbourne University. A series of thirty-one cadavers was examined. Fifty-three sinuses were carefully identified. In eight cases both right and left sinuses passed over the cranial surface of the fifth nerve root. In three cases both right and left sinuses passed under the root. In three cases the sinus divided on both sides, portion passing under and portion passing over the root. Of the total number thirty sinuses passed over the root, twelve passed under the root, and thirteen divided lateral to the root, portion passing over and portion passing under the root, then reuniting to join the cavernous sinus. Seven sinuses could not be identified owing to the condition of the skulls.

I wish to thank Prof. F. Wood-Jones for advice and Dr E. Ford for assistance in collecting material for this investigation.

REVIEWS

The Digestive Tract: A Radiological Study of its Anatomy, Physiology and Pathology. By A. E. Barclay, O.B.E., M.D., D.M.R.E. (London: Cambridge University Press.) 1933. Pp. xxviii + 396, 275 figures. Price 36*s.* net.

Dr Barclay has provided anatomists, who use X-rays in the teaching of the subject, with a much needed volume of reference which cannot but be of the greatest value in their work. The plan superimposing the radiological appearance of the several parts of the alimentary tract on actual photographs of the patient demonstrates the wide limits of the "normal" digestive organs and also enables one to appreciate, as Dr Barclay has pointed out, the influence which sensory stimuli and emotional states, and also posture and respiration, have on the form and position of these organs. Arising out of these observations, the author takes pains to point out that "there is no such thing as 'normal'" when applied to the abdominal organs.

Anatomists will read with interest, even if they disagree with the thesis, that there is no "fixity" of position or form of viscera nor are there any "fixal points" relating the viscera to the abdominal wall. The movements of the food during its passage through the canal are considered in detail and are worthy of careful study.

The radiological appearance in disease and the details of equipment form valuable chapters which are written, like the rest of the book, in a concise, practical, and thoughtful way. The illustrations are admirable and the bibliography complete.

Histology. By S. Ramón-Cajal, M.D. (Madrid), F.R.S. (London), LL.D. (Clarke), revised by J. F. Tello-Múñoz, M.D. (Madrid). Authorised translation from the tenth Spanish edition by M. Fernán-Núñez, M.D. (Madrid). (London: Baillière, Tindall and Cox.) 1933. Pp. xiv + 738, 535 figures. With index and appendix. Price 40*s.* net.

The translation of Cajal's text-book of histology for students is not only a matter of interest but an achievement for which all will be grateful.

Cajal's unchallenged eminence in histology must have made everyone concerned with the subject wonder how he handed it on to his students. The translation from the Spanish text by M. Fernán-Núñez makes the answer accessible to everyone. It is natural that the emphasis should be placed on neuro-anatomy, and this aspect of the subject occupies a greater proportion of the book than is found in corresponding English works. There is an abundance of excellent illustrations and every part of the subject, even when the treatment is brief, contains an adequate account of present-day knowledge.

The conception of histology is strictly anatomical, and this limitation is imposed by the definition of the subject expressed by Cajal. It is general anatomy—the structure of the cells and tissues common to most organisms. The text nowhere includes paragraphs on histo-physiology, a feature of many of the most recent publications. Besides giving a concise account of Cajal's labours in neuro-anatomy, the book also, in its compendium of methods, gives the silver procedures used in the Madrid laboratory with the comments of the author on their value.

The translator had no doubt considerable difficulties to contend with. He has adopted the method of following closely the author's text, and perhaps a literal translation is the only way of dealing with a scientific treatise. Though the reading of many sentences is not always smooth and easy, yet there is nowhere any real difficulty in grasping their meaning.

The Distribution of the Currents of Action and of Injury displayed by Heart Muscle and other Excitable Tissue. By F. N. Wilson, A. G. Macleod, and P. S. Barker. University of Michigan Studies, Scientific Series, vol. x. (Ann Arbor: University of Michigan Press.) 1933. Pp. viii + 59. Price $1.50 (postage extra).

This monograph starts by stating that the majority of studies that have been concerned with the more fundamental problems presented by bioelectric phenomena have been carried out upon isolated tissues suspended in air. The authors go on to say that the results of such studies cannot be applied without modification to the interpretation of the electric phenomena manifested by tissues *in situ*. The investigations carried out by the authors were directed mainly to the auricle of the mammalian heart and the ventricle of the reptilian heart, these suffering no anatomical disturbance other than the necessary incisions to expose them.

Craib previously had raised the problem of the differences in electric responses obtained from a tissue immersed in a conducting medium, or surrounded by a dielectric like air. The present authors have by their investigations obtained similar results and use Craib's theory of doublets or dipoles to explain these.

The book offers an exposition of the physics and mathematics which govern the distribution of electric currents in volume conductors. The currents produced by the heart beating *in situ* they regard as being in accordance with such conceptions. They find that by leading off to the string galvanometer, from one electrode in contact with the heart and from the other upon an extremity, the resulting curve can be considered as a record of the electrical changes at the cardiac electrode alone. The curves obtained from certain auricular regions by this method are found to be relatively simple; simple curves are also obtained by this method after injury, and both can be explained on the theory of primary and secondary doublets or dipoles. From a theoretical study of the electrical field produced by a polarised membrane they infer that the observed distribution of the currents of action and of injury produced by cardiac muscle and other excitable tissues immersed in an extensive conducting medium are reconcilable with the classical membrane theory. In the case of an injured muscle fibre the electric field produced is approximately equivalent to that which would be produced by polarisation of the surface which separates the injured from the uninjured tissue.

An Introduction to the Study of the Nervous System. By E. E. Hewer, D.Sc. and G. M. Sandes, F.R.C.S. (London: William Heinemann (Medical Books) Ltd.). 1933. Pp. xiv+147, 65 diagrams. Price 21*s*. net.

The second edition of this text-book has been enlarged by additions to the sections dealing with the corpus striatum, diencephalon, autonomic nervous system, and the blood vessels of the central nervous system. As in the first edition, the simple and clear diagrams form the chief asset of this book. The text is condensed and at times rather obscure (especially the section on these membranes and vessels of the brain). We would criticise (among other things) the position of fibres of the "fillet group" at the anterior extremity of the internal capsule (Diagram 13), the limitation of cortico-positive fibres to such small parts of the frontal and temporal lobes, the inclusion of thalamo-olivary and thalamo-spinal tracts (which for some years now have been recognised to be probably of pallidal origin), the representation of visceral impulses terminating in the post-rolandic cortex (Diagram 26), and the connections of the anterior and medial thalamic nuclei with the subthalamic nucleus.

It would be pleasant, also, to see the last of the antiquated misconception that the medial nucleus of the thalamus is the "oldest part" of this structure. It is very much the reverse.

Practical Anatomy. By Six Teachers, edited by E. P. Stibbe, F.R.C.S. (London: Edward Arnold and Co.) 1932. Pp. x+719 with 330 diagrams. Demy 8vo. Price 30*s.* net.

Text-books of Practical Anatomy are not numerous, and this one is intended to replace one which was edited by Parsons and Wright. It is refreshing to read a book in which the arrangement is regional and the "old" nomenclature is still used. With the possibility of a shorter time to be devoted to anatomy, minute detail in dissection must go. This book provides a complete course in practical anatomy for any examination including the Primary Fellowship of the Royal College of Surgeons. Perhaps one of the features of this book is the abundance of excellent illustrations, mostly from the pen of Miss Mary Barclay-Smith. Original drawings are always a great asset in the teaching of practical anatomy. A one-volume book of convenient size has many advantages over two volumes.

THE MORPHOLOGY OF THE FORE-BRAIN ARTERIES, WITH ESPECIAL REFERENCE TO THE EVOLUTION OF THE BASAL GANGLIA

By A. A. ABBIE, M.B., B.S., B.Sc. (Sydney)[1]
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The morphology of the cerebral arteries has been investigated in particular by Hofmann (1) and de Vriese (2), who regarded the vessels merely as an isolated morphological unit and failed to correlate changes in vascular pattern with any evolutionary progress in the brain itself. Shellshear, in many papers (3, 4, 5, 6, 7, 8), has claimed that the arteries together with the brain constitute a single functional unit, a neurovascular mechanism of which neither component is independent of the other. He has shown that the arteries are constant in their terminal supply; consequently the evolution of the vessels is dependent upon, and proceeds hand in hand with, the evolution of their field of distribution.

A survey of the literature relating to cerebral blood supply reveals a great amount of variation and apparent contradiction of the principle of vascular constancy. Much of this apparent incompatibility is due to the failure to appreciate the significance of the principles of economy of distribution and convenience of source. These have been discussed briefly in previous papers (9, 10); here they will be exemplified more fully. We may say that the brain and its blood supply are not independent variables, the arteries of the brain are as much a part of the neurovascular mechanism as is the brain itself; any change in brain structure is reflected in an equivalent alteration in its blood supply. Thus the two components of this mechanism evolve in harmonious co-operation. As the brain expands to meet new situations, its arteries extend to satisfy the increased functional demand. Cerebral evolution would not be possible were it not accompanied by a corresponding evolution in the vascular pattern.

The following work was undertaken to determine the blood supply of the brain in as complete a phylogenetic series as was available. It is considered that the results form a complete vindication of the principle of vascular constancy, that principle first dimly visualised by Guyot in 1825 (11), stated as an explicit law by Duret in 1874 (12), and since reaffirmed by Shellshear.

MATERIAL AND METHODS

The brains studied were of every vertebrate phylum from Fish to Man, but excluding Birds. The Fish was a single brain of *Squalus acanthias* which had been preserved in formalin for some time. For Amphibia, four brains of *Rana temporaria* were used, and of Reptiles one *Sphenodon* and two crocodile brains were studied. The mammalian series included two Marsupials (*Macropus*

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thetidis and *M. eugenii*); one Rodent (*Castor canadensis*); one Carnivore (*Cynaelurus jubatus*); several Ungulates including four sheep (*Ovis aries*), one reindeer (*Rangifer tarandus*), one kudu (*Strepsiceros strepsiceros*) and one tapir (*Tapirus terrestris*); one lemur (*L. variegatus*); six apes including species of *Lagothrix*, *Papio*, *Cercopithecus* and *Macacus*; and forty human brains. The frog brains were injected with Indian ink, the *Sphenodon* with carmine gelatine, and in those mammalian brains available for dissection the anterior choroidal artery was generally injected with Indian ink.

The arteries of the various brains were first studied in their surface distribution and subsequently dissected in the frog, crocodile, Marsupial, sheep, reindeer, lemur, ape and Man. Both hemispheres were used, and some of the hemispheres of each type were cut horizontally and others coronally in sections to ensure accuracy of localisation. In the dissections the arterial branches were followed individually to their destinations with the aid of a binocular microscope.

The vessels of the brain of the dogfish, frog, tuatara, sheep and Man will be described in detail. Those of the other types will be discussed only in so far as they conform to, or appear to contradict, the theory of constancy in the vascular pattern of the fore-brain.

DOGFISH (*SQUALUS ACANTHIAS*)

Hofmann (1) and Kappers (13) have both studied the cerebral vessels of Fishes and describe a medial and a lateral olfactory artery passing forwards to the fore-brain from the cranial division of the internal carotid artery. In fig. 1 these vessels can be seen running along the medial and lateral borders of the hemisphere to the anterior aspect; they are related more to the ventral than the dorsal half of the hemisphere and, by small anastomotic channels, form a closed vascular ring just ventral to the horizontal equator. The main vessels also communicate with each other dorsally and ventrally to form a closed network which holds the hemisphere within its meshes. Thus the medial and lateral olfactory arteries are not, indeed, separate arteries, they are merely channels in a closed primitive vascular net which have enlarged in response to a specific functional demand.

Many writers—Elliot Smith (14, 15), Dart (16) and others—have shown that the ventral part of the Fish brain is more primitive than the dorsal. Dart calls it the palaeo-olfactorium, and has shown (17) that from its cortical cells have developed the tuberculum olfactorium, the islets of Calleja, the nucleus of the diagonal band of Broca, the anterior olfactory nucleus of Johnston (18) and the palaeo-striatum. The dorsal part forms the neo-olfactorium comprising the primordia of the pyriform cortex, hippocampus and hypopallium.

The medial and lateral olfactory arteries form a vascular ring around the palaeo-olfactorium and lie in medial and lateral grooves which separate it from the neo-olfactorium. The vascular channels over the palaeo-olfactorium are larger than those over the neo-olfactorium, as would be expected in view of

the greater functional activity of the former in this primitive brain. A simple schematic section through the anterior part of the hemisphere of such a brain (fig. 2) shows the medial and lateral olfactory arteries related to their respective

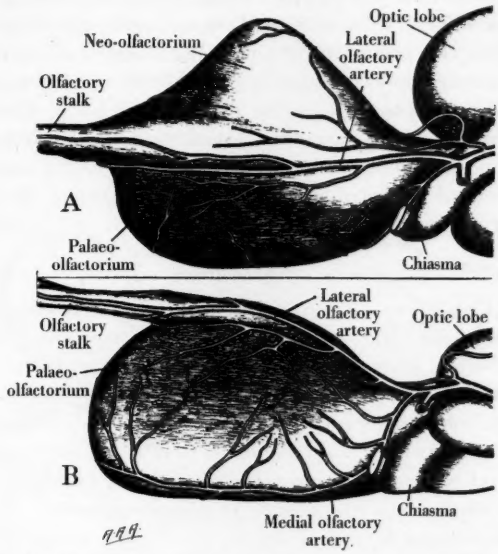

Fig. 1. The arteries of the brain of the dogfish (*Squalus acanthias*). A, left lateral aspect; B, ventral aspect of left hemisphere.

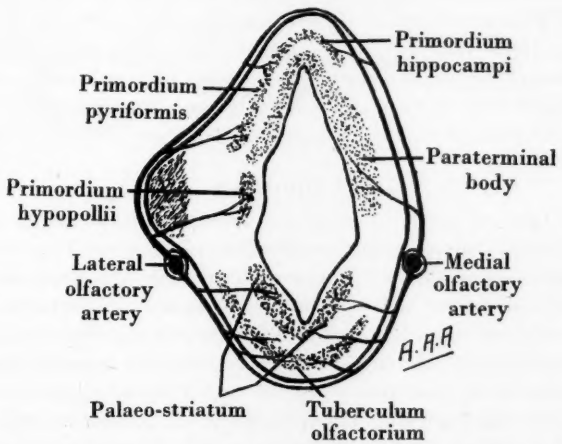

Fig. 2. Schematic section through the anterior part of the right hemisphere of the dogfish brain showing the relation of the lateral and medial olfactory arteries to the neo- and palaeo-olfactoria.

grooves and connected dorsally and ventrally by small channels. In the ventral part lie the cortex of the palaeo-olfactorium and the palaeo-striatum; in the dorsal the primordia of the pyriform lobe, hippocampus and hypopallium. The palaeo-olfactorium is supplied medially from the medial, and laterally from the lateral olfactory channel; in the neo-olfactorium the lateral olfactory channel supplies the primordia of the hypopallium and pyriform area and most of that of the hippocampus, the medial channel the most medial part of the primordium hippocampi and the paraterminal body. It will be observed that those channels which have been called the medial and lateral olfactory arteries are almost symmetrically disposed and present the simplest and most economical method of distributing blood to all parts of the brain through their subsidiary branches.

Summary

1. In the Fish there is a simple cerebral hemisphere composed chiefly of palaeo- and neo-olfactoria. These are separated medially and laterally by slight grooves which lie just ventral to the horizontal equator.

2. The arterial supply is maintained through a closed primitive vascular network which holds the brain within its meshes.

3. From this network certain channels have enlarged to support the chief burden of blood carriage. These are the medial and lateral olfactory arteries related to the medial and lateral grooves described above.

4. The medial and lateral olfactory arteries are symmetrically placed so that all parts of the brain are within easy reach of either. This forms the most economical method of blood distribution.

5. The lateral olfactory artery supplies the structures which are nearest: the lateral part of the palaeo-olfactorium and the primordia of the hypopallium, pyriform lobe and most of that of the hippocampus. The medial olfactory artery reaches the medial part of the palaeo-olfactorium, the paraterminal region and the medial part of the primordium hippocampi. The blood supply to the palaeo-olfactorium is richer than that to the neo-olfactorium.

AMPHIBIA

In the frog, as in the dogfish, the internal carotid artery divides into cranial and caudal divisions at the side of the hypophysis. The cranial division (fig. 3) passes forwards over the optic tract at whose anterior border it divides into medial and lateral olfactory branches. It is evident that these are not quite the same as the medial and lateral olfactory arteries of the dogfish. In the Fish the lateral olfactory artery arises from the cranial division at the lateral border of the hemisphere; in the frog it takes origin from one of the arteries to the diencephalon. The hemisphere has grown posteriorly over the diencephalon and the artery has simultaneously shifted its site of origin. No new artery has appeared, this anastomotic channel between the telencephalic and diencephalic arteries was present in the dogfish. The channel has merely

enlarged to provide a closer source of blood for the lateral olfactory artery. This vessel passes forwards over the dorso-lateral aspect of the hemisphere and ends on the lateral border of the olfactory stalk by anastomosing with branches of the medial olfactory artery.

In its passage anteriorly the lateral olfactory artery gives off many fairly large branches which reach structurally differentiated portions of the hemisphere. Some pass to the dorso-medial aspect of the telencephalic wall to supply most of the primordium hippocampi. These also reach the posterior part of the paraterminal body and anastomose anteriorly with branches of the medial

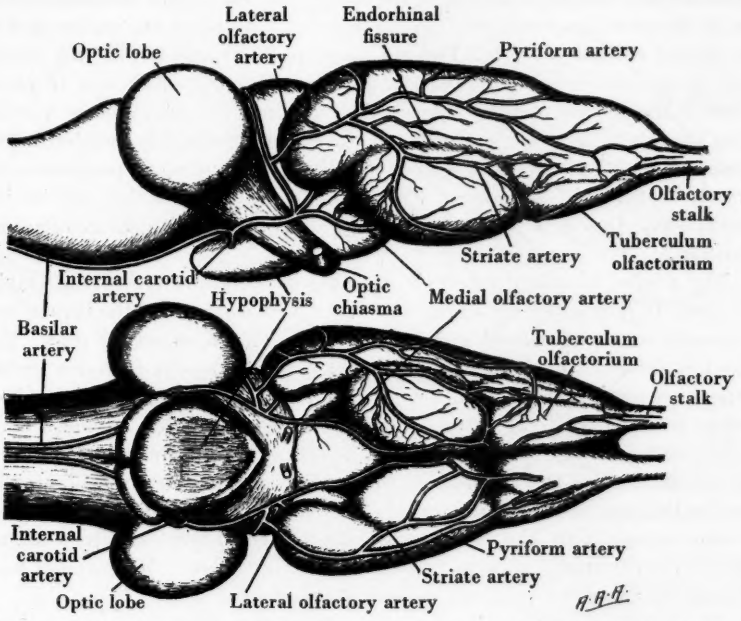

Fig. 3. The arteries of the brain of the frog (*Rana temporaria*). Note that the lateral olfactory artery arises from a diencephalic stem.

olfactory artery. They may be called hippocampal arteries. The main channel of the lateral olfactory artery runs forwards over the primordium pyriformis to anastomose with the medial olfactory branches to the olfactory stalk. This is the pyriform artery. The next large branch passes ventrally and then anteriorly in the groove between the primordium pyriformis and the ventro-lateral wall of the hemisphere to anastomose anteriorly with branches of the medial and lateral olfactory arteries over and around the tuberculum olfactorium. This is the striatal artery. Finally, a large arterial channel runs from the striatal artery across the ventral part of the hemisphere to join the medial olfactory artery.

The lateral olfactory artery has progressed beyond the condition of the similarly named vessel of the dogfish. The only representative of this is the striatal artery running forwards in the groove between the primordium pyriformis and the ventro-lateral wall of the hemisphere. The primordium pyriformis is part of the neo-olfactorium, the ventro-lateral wall part of the palaeo-olfactorium and the groove between is the endorhinal fissure of Elliot Smith or the sulcus palaeo-olfactorius lateralis of Dart. Thus, the striatal artery of the frog is the representative of the lateral olfactory artery of the dogfish. It maintains its old connection with the cranial division through the rich anastomosis at the posterior end of the endorhinal fissure. The neo-olfactorium has so increased its functional development that it claims the major part of the lateral olfactory artery. The old anastomotic channels over the dorsal part of the hemisphere have enlarged to carry the increased flow of blood which is more conveniently supplied directly from the diencephalic vessels. Thus the lateral olfactory artery has become more exclusively devoted to the growing neo-olfactorium and is evolving definite pyriform, hippocampal and striatal branches in accordance with the differentiation of this part of the hemisphere. It will be seen that it still retains some of its palaeo-olfactory branches.

The medial olfactory artery is the anterior continuation of the cranial division. It runs anteriorly along the ventro-medial border of the hemisphere to anastomose with lateral olfactory branches on the olfactory stalk. This vessel is related more closely to the palaeo-olfactorium and retains its old disposition almost unchanged. The greater relative growth of the neo-olfactorium has displaced the artery somewhat ventrally so that it comes to lie at the ventro-medial border instead of at the medial equatorial groove. On the medial wall of the hemisphere the medial olfactory artery still supplies most of the paraterminal body and the anterior end of the hippocampus where it anastomoses with hippocampal branches of the lateral olfactory artery. The primitive arterial network remains intact, but more of its channels have enlarged to carry the increased volume of blood demanded of them.

The brain of existing Amphibia, as shown by Elliot Smith (20), closely resembles that of a lowly dipnoan. Kappers (21) and Herrick (22) in particular have described the amphibian brain and Hines (23) has shown how closely it resembles a developmental stage of higher brain forms. It is possible to distinguish the neo- and palaeo-olfactory areas of Dart; to these Johnston (19) has added a primitive general cortex. The palaeo-olfactorium contains the paraterminal body, tuberculum olfactorium and nucleus of the diagonal band, and the palaeo-striatum. The neo-olfactorium comprises the primordia of the pyriform lobe, hippocampus and hypopallium, but Kappers calls the last epistriatum (25) after the nomenclature of Edinger (26).

In fig. 4 are shown schematic sections through the anterior and posterior parts of the hemisphere of the brain of the frog indicating the relation of the arteries to the principal cell masses. It will be seen that the medial olfactory

artery still supplies the medial part of the palaeo-olfactorium containing the medial portions of the tuberculum olfactorium, nucleus of the diagonal band and palaeo-striatum. In consequence of the ventro-lateral shift of the main bulk of the medial olfactory artery, some of the channels to the lateral part of the palaeo-olfactorium come to receive their blood from the medial rather than from the lateral olfactory artery, so that most of the lateral aspect of the palaeo-olfactorium is also supplied from the medial olfactory artery. Thus the ventro-lateral part of the tuberculum olfactorium and the ventral aspects of the palaeo-striatum and the primitive amygdala are supplied from the medial olfactory artery, but the lateral olfactory artery retains its distribution

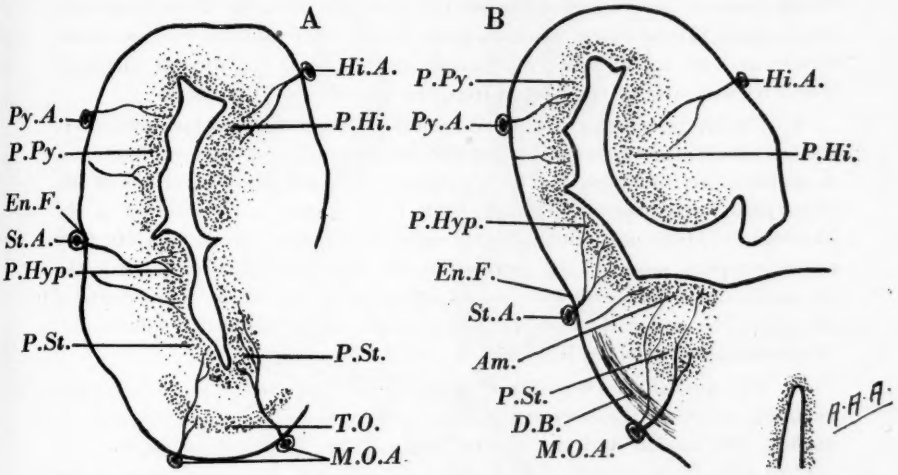

Fig. 4. Schematic sections through A the anterior and B the posterior parts of the right hemisphere of the frog, showing the relation of the arteries.

Am. amygdala; *D.B.* diagonal band; *En.F.* endorhinal fissure; *Hi.A.* hippocampal artery; *M.O.A.* medial olfactory artery; *P.Hi.* primordium hippocampi; *P.Hyp.* primordium hypopallii; *P.Py.* primordium pyriformis; *P.St.* palaeo-striatum; *Py.A.* pyriform artery; *St.A.* striate artery; *T.O.* tuberculum olfactorium.

to the dorsal parts of these structures. In one case the branches from the medial olfactory artery to the primitive amygdala and posterior part of the palaeo-striatum were represented by a single large trunk instead of a series of small vessels. The paraterminal body still obtains most of its blood from the medial olfactory artery which thus retains this portion of its palaeo-olfactory field.

The neo-olfactorium receives most of its blood through the hippocampal, pyriform and striatal branches of the lateral olfactory artery. The hippocampal artery supplies most of the primordium hippocampi and anastomoses anteriorly with the hippocampal and paraterminal branches of the medial olfactory artery. The pyriform artery supplies all the primordium pyriformis and the

striatal artery all the primordium hypopallii as well as the dorso-lateral derivatives of the palaeo-olfactorium.

Thus the arteries of the amphibian brain are strictly comparable with those of the Fish; the various changes observed can be attributed to the increased cerebral development of the amphibian.

Summary

1. In the frog the primitive arterial network is maintained.

2. In this network it is possible to discern the original enlarged channels which, in the dogfish, were known as the medial and lateral olfactory arteries. Other channels have enlarged to meet the increased demands of the structures they supply. These extra demands come almost entirely from the neo-olfactorium and are satisfied by enlargement of the dorsal anastomotic channels which receive most of their blood from the lateral olfactory artery.

3. The lateral olfactory artery comprises a striatal branch which represents the lateral olfactory artery of Fishes, and hippocampal and pyriform branches. A nearer source of supply has been provided by the opening up of one of the diencephalic anastomotic channels, while the old stem is represented in the anastomoses at the posterior end of the endorhinal fissure. The lateral olfactory artery supplies most of the primordium of the hippocampus and all the primordia of the pyriform lobe and hypopallium as well as the dorsal parts of the primitive amygdala and the lateral parts of the striatum, tuberculum olfactorium and diagonal band.

4. The medial olfactory artery supplies most of the palaeo-olfactorium including most of the tuberculum olfactorium and diagonal band and its nucleus, the medial and the ventral parts of the palaeo-striatum and the ventral part of the primitive amygdala. In addition, it supplies most of the paraterminal body and the anterior end of the hippocampus.

REPTILIA

The following account is based upon the examination of a single *Sphenodon* brain, the arteries having been injected with carmine gelatine. The arteries of the brains of two crocodiles were studied to supplement the information thus obtained. In addition, there was a series of coronal sections through the whole head of a young *Sphenodon* which were 250 μ thick, stained with eosin and haematoxylin. In these it was possible to trace the terminal arteries to the various cell masses.

The cerebral arteries of *Sphenodon* have been well described by Dendy (27), those of various Reptiles by Hofmann (1) and Kappers (13), and of the crocodile by Shellshear (7). In this account special attention will be paid to the functional differentiation of the vessels.

In fig. 5 A the arteries of *Sphenodon* are seen from the ventral aspect. The internal carotid artery divides at the side of the hypophysis into cranial and caudal divisions. Near its origin the cranial division gives off the posterior

cerebral artery and, near the posterior end of the endorhinal fissure, the inferior cerebral artery of Dendy. Slightly anterior to this the middle cerebral arises, while the anterior continuation of the cranial division constitutes the anterior cerebral artery.

The posterior cerebral artery runs dorsally between the posterior pole of the hemisphere and the optic lobe to the dorso-medial border of the hemisphere and proceeds along this to the anterior pole. In its course it supplies

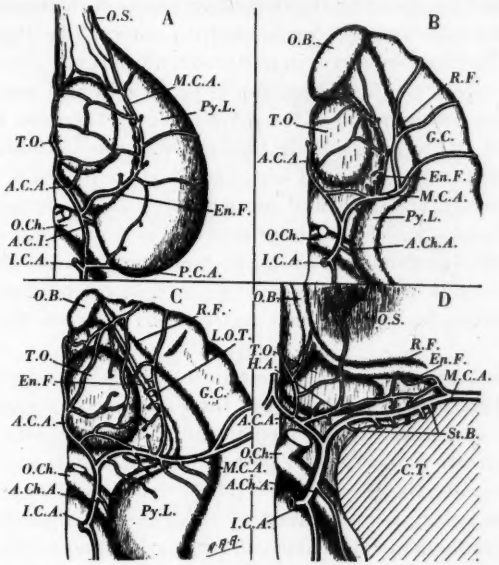

Fig. 5. The arteries of the base of the brain of: A, *Sphenodon*; B, a marsupial (*M. thetidis*); C, an ungulate (*S. strepsiceros*); D, a Primate (*C. sabaeus*); showing the relation of the anterior and middle cerebral arteries to the palaeo-striatum, and the formation of Heubner's artery.

A.C.A. anterior cerebral artery; *A.C.I.* inferior cerebral artery; *A.Ch.A.* anterior choroidal artery; *C.T.* cut surface of temporal lobe; *G.C.* general cortex; *En.F.* endorhinal fissure; *H.A.* Heubner's artery; *I.C.A.* internal carotid artery; *L.O.T.* lateral olfactory tract; *M.C.A.* middle cerebral artery; *O.B.* olfactory bulb; *O.Ch.* optic chiasma; *O.S.* olfactory stalk; *P.C.A.* posterior cerebral artery; *Py.L.* pyriform lobe; *R.F.* rhinal fissure; *St.B.* striate branches; *T.O.* tuberculum olfactorium.

branches to the anterior part of the optic lobe and to the posterior part of the pyriform lobe, there to anastomose with branches of the middle cerebral artery. It also supplies the choroid plexus of the third and lateral ventricles. As the artery passes along the dorso-medial border it supplies the upper part of the pyriform lobe anastomosing with branches of the middle cerebral artery, but its main supply is to the hippocampal formation. A few branches reach the posterior part of the paraterminal body. At the anterior end of the hippocampus the posterior cerebral artery anastomoses with hippocampal and paraterminal branches of the anterior cerebral artery, and over the primordium

neopallii—the newly formed "general cortex" of Crosby (28)—it enters into anastomosis with branches of the anterior and middle cerebral arteries, as Shellshear showed for the crocodile.

The inferior cerebral artery passes dorsally between the hemisphere and optic tract to reach the posterior part of the corpus striatum.

The middle cerebral artery runs laterally to the endorhinal fissure to which it is closely applied in its anterior course. At the anterior pole of the hemisphere this vessel passes on to the dorso-lateral aspect of the olfactory stalk. In its passage it supplies many branches to the pyriform lobe, these anastomose with posterior cerebral branches; in particular, there is one very large anastomotic union between pyriform branches of the middle and posterior cerebral arteries over the posterior end of the pyriform lobe. The main channel of the middle cerebral artery passes along the endorhinal fissure and supplies perforating branches to the pyriform lobe, endorhinal fissure and lateral part of the palaeo-olfactorium. Over and around the palaeo-olfactorium is a rich series of anastomotic vessels between the middle and anterior cerebral arteries. The middle cerebral artery ends by anastomosing over the dorso-lateral aspect of the olfactory stalk with branches of the anterior cerebral artery, and over the general cortex in the common anastomosis between the three major arteries.

The anterior cerebral artery runs anteriorly along the ventro-medial border of the hemisphere to about the level of the tuberculum olfactorium where it bends dorsally and passes to the medial wall of the hemisphere. On its way it supplies branches to the medial part of the palaeo-olfactorium and some which pass laterally to join middle cerebral branches. The general anterior direction of the artery is maintained by small branches which run forwards along the medial border of the palaeo-olfactorium and on to the medial aspect of the olfactory stalk to anastomose with branches of the middle cerebral artery. From these small branches, too, twigs are given to the medial part of the palaeo-olfactorium and also anastomotic branches to the middle cerebral artery. The main trunk of the anterior cerebral artery passes to the medial wall of the hemisphere to supply the anterior part of the hippocampus and most of the paraterminal body (anastomosing with the posterior cerebral artery) and ends in the common anastomosis over the primordium neopallii.

The first significant work on the cell masses of *Sphenodon* was published in 1902 (20) and in 1919 (29) by Elliot Smith when he described the hypopallium in its relationship to the pyriform cortex and lateral striate arteries. Subsequently, Cairney (30) and Durward (31) gave more complete accounts of the structure of the *Sphenodon* brain. The fore-brain can be divided into palaeo-olfactorium and neo-olfactorium. The palaeo-olfactorium contains the tuberculum olfactorium, paraterminal body, the diagonal band and its nucleus and the palaeo-striatum. The neo-olfactorium includes the well-developed hippocampus, pyriform lobe and hypopallium; the hypopallium has been subdivided by Dart, Johnston and others into hypopallium anterius related to the

"general cortex" and hypopallium posterius related to the pyriform cortex and amygdala (the archistriatum of Kappers). In addition, the primordium neopallii lies anteriorly on the dorso-lateral aspect of the hemisphere, interposed between hippocampus and pyriform lobe.

In fig. 6 is shown a series of sections through a *Sphenodon* brain. In these the relationship of the terminal arteries to the cell masses is clearly depicted. In the first section the inferior cerebral artery arises from the cranial division of the internal carotid artery and, entering the brain substance, passes dorsally

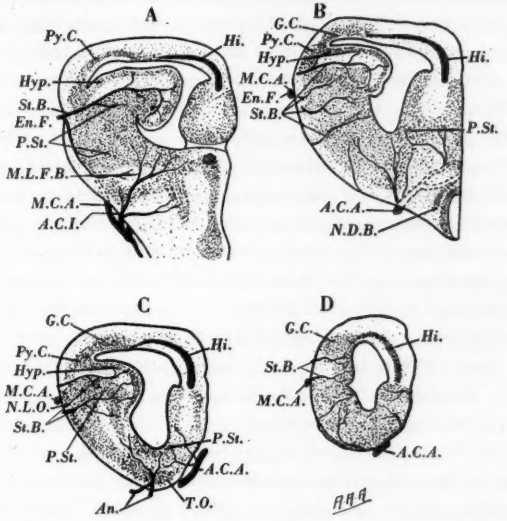

Fig. 6. A series of sections of the brain of a young *Sphenodon* from behind forwards, cut at 250 μ and stained with eosin and haematoxylin. The sections are cut obliquely so that the upper part is well anterior to the lower.

A.C.A. anterior cerebral artery; *A.C.I.* inferior cerebral artery; *An.* anastomosis over the tuberculum olfactorium; *En.F.* endorhinal fissure; *G.C.* general cortex; *Hi.* hippocampus; *Hyp.* hypopallium; *M.C.A.* middle cerebral artery; *M.L.F.B.* medial and lateral fore-brain bundles; *N.D.B.* nucleus of diagonal band; *N.L.O.* nucleus of lateral olfactory tract; *P.St.* palaeo-striatum; *Py.C.* pyriform cortex; *St.B.* striate branches; *T.O.* tuberculum olfactorium.

through the fore-brain bundles to the ventro-medial part of the primitive amygdala and the associated part of the palaeo-striatum; more dorsally branches of the middle cerebral artery enter the palaeo-olfactorium to supply the dorso-lateral parts of these structures. These middle cerebral branches also supply the whole of the hypopallium—in this case hypopallium posterius. The next section, anterior to the last, shows the anterior cerebral artery, passing medially. On its way it gives branches to the ventral and medial parts of the primitive amygdala and the palaeo-striatum, the nucleus of the diagonal band and the paraterminal body. The middle cerebral artery lies in

relation to the endorhinal fissure and its branches enter the brain through the pyriform cortex, through the fissure itself and through the dorsal part of the palaeo-olfactorium. In general it may be said that the striate branches of the middle cerebral artery fall into three groups. Those which pierce the pyriform cortex pass just dorsal to the nucleus of the lateral olfactory tract to reach the dorsal fold of the hypopallium; those which pass through the endorhinal fissure (these are most numerous and constitute the lateral striate arteries of Elliot Smith) to supply the dorsal part of the palaeo-striatum and primitive amygdala and the most medial fold of the hypopallium; the branches which enter the palaeo-olfactorium ventral to the endorhinal fissure supply the dorso-lateral parts of the primitive amygdala and palaeo-striatum.

The third section lies anterior to the amygdala and passes through the tuberculum olfactorium. Here the main stem of the anterior cerebral artery lies close to the paraterminal body which it supplies, and sends branches to the palaeo-striatum. Over the tuberculum olfactorium there is an anastomotic union between branches of the anterior and middle cerebral arteries. From this vessels pass to the tuberculum and to the ventral part of the palaeo-striatum. The middle cerebral artery lies close to the endorhinal fissure and its branches pass to the hypopallium and the dorsal part of the palaeo-striatum. The fourth section lies still more anteriorly. It shows a branch of the anterior cerebral artery supplying nearly all the palaeo-olfactorium in this region and also the most ventral part of the anterior hippocampus. Branches of the middle cerebral artery reach the "general cortex" and the hypopallium anterius. In these sections the posterior cerebral artery is not drawn, as its simple relation to the hippocampus requires no further elaboration.

In relation to the manner in which the striate branches enter the brain to reach the hypopallium, Johnston (18) states (p. 355) that the vessels which supply the caudate nucleus frequently pierce the pyriform cortex, although he agrees that the majority of these arteries actually enter the endorhinal fissure. As shown above (fig. 6), several of the middle cerebral branches certainly pass through the pyriform cortex—mostly dorsal to the nucleus of the lateral olfactory tract—and these are devoted mainly to the more dorsal fold of the hypopallium. They will be considered further in relation to the mammalian striatum. It may be mentioned that branches of the middle cerebral artery could be traced into the most anterior part of the hypopallium although Durward states that he was unable to find such arteries.

The posterior cerebral artery is related to the dorsal part of the pyriform lobe and most of the hippocampus and represents the hippocampal artery of the frog. Its origin has, however, been shifted posteriorly with the backward expansion of the hemisphere and a still more posterior diencephalic artery has been employed as the most convenient stem. In addition, the posterior cerebral artery uses the same parent stem to supply blood to the choroid plexus and the anterior part of the optic lobe. It has "taken over" the blood supply of these regions. The origin of the lateral olfactory artery of the frog

persists in the large anastomotic channel between the posterior and middle cerebral arteries over the posterior part of the pyriform lobe—a connection which is never lost. Hofmann regarded the lateral olfactory artery of the frog as a posterior cerebral artery and called it the *arteria cerebralis posterior* α, but this homology cannot be entirely correct because the posterior cerebral artery of *Sphenodon* represents only the hippocampal branch of the lateral olfactory artery of the frog.

The inferior cerebral artery supplies the posterior parts of the palaeostriatum and primitive amygdala. In the crocodile (9) there is no separate inferior cerebral artery. It is represented by a series of minute anastomotic channels arising from the stem of the carotid artery and running posteriorly along the optic tract to join the posterior cerebral artery. In the specimen of *Sphenodon* which I examined such a connection probably existed but was uninjected and so the inferior cerebral artery appeared to be a discrete vessel. I suggest that this is the true arrangement in all Reptiles and consider that my previous description was only partly correct (9). In *Sphenodon* there is no separate inferior cerebral artery, the vessel which was so named by Dendy is the anterior part of this anastomotic chain which has become enlarged in response to the greater functional demands made upon it by the palaeostriatum. I had previously homologised this anastomotic chain of Reptiles with the anterior choroidal artery of Mammalia and this I still believe to be correct. The inferior cerebral artery is the enlarged anterior part of the anastomosis between the cranial division of the internal carotid artery and the posterior cerebral artery and its predecessor is to be found in the series of similar anastomoses in this region in the frog (fig. 3). Thus the primitive vascular network is still intact and no new arteries have been introduced.

The middle cerebral artery is closely related to the endorhinal fissure and supplies the pyriform lobe and the lateral part of the palaeo-olfactorium as well as the whole of the hypopallium and the dorsal part of the palaeostriatum. Clearly, its main trunk represents the striatal branch of the lateral olfactory artery of the frog and all of the lateral olfactory artery of the dogfish. In addition, it includes pyriform branches of the frog which were not developed to any degree in the dogfish. Kappers (13) has noted this similarity and homologises the lateral olfactory artery of Fishes with the middle cerebral artery of Reptiles. There is considerable justification for this homology, but to make it complete it is necessary to add to the lateral olfactory artery of Fishes the pyriform artery of Amphibia. The two vessels together represent the middle cerebral artery of higher animals.

The brain of existing Amphibia is known to be specialised and regressive. It remains to be decided whether the brain is the survivor of an aberrant form off the main line of evolution which passed from Fish to Reptile, or whether it is the living representative of a ?Stegocephalian ancestor intermediate between Fish and Reptile and now extinct. The arteries give some clue to the interpretation of the status of the brain of the frog. The posterior cerebral

artery is obviously developed from the hippocampal artery of a lower form, but the origin of the middle cerebral artery presents a difficulty. It has evolved from the lateral olfactory artery of Fishes, retaining the origin and course of this vessel but has acquired pyriform branches. Such pyriform branches are found in the frog, but there they arise from the more dorsal development of the lateral olfactory artery—the stem and hippocampal branches of which represent the posterior cerebral artery of Reptiles. In the frog the striatal artery—the first representative of the middle cerebral—also takes origin from this potential posterior cerebral artery, its old direct connection with the cranial division of the internal carotid artery surviving as a few anastomotic channels at the posterior end of the endorhinal fissure. The differentiation of the cerebral arteries of the frog suggests a corresponding evolution of the parts they supply, and these arteries present all the cardinal channels necessary for the formation of the cerebral arteries of higher animals. It would appear that the frog is the degenerated descendant of an ancestor which possessed the potentialities for laying down the cerebral vascular pattern of higher animals. Such an ancestor had representatives of separate anterior, middle and posterior cerebral arteries. From this intermediate condition the vascular pattern of modern Reptiles has evolved, but the brain of existing Amphibia has so degenerated that the precursor of the middle cerebral artery has lost its need for a rich blood supply to the striatal region and its direct connection with the cranial division has dwindled to the remaining anastomotic channels. Evolution thus appears to have passed from Fish to Reptiles through a now extinct intermediate ancestor, from this common ancestor the frog has degenerated to its present regressive condition.

In the crocodile, as shown by Shellshear, the middle cerebral artery is not a single large vessel but is represented by a series of smaller anastomotic channels. This fact is not noted in the Reptiles described by Hofmann and Kappers, nor does it appear to hold in Birds. It may reflect a still unsettled condition of the striatal region in crocodiles.

The anterior cerebral artery presents a simpler problem. This vessel is the descendant of the medial olfactory artery of Fishes and Amphibia. One great change in volume of distribution, however, demands attention. In lower animals the main trunk of the medial olfactory artery passes to the olfactory stalk, but in Reptiles the greater part of the blood is diverted to the medial wall of the hemisphere—to the paraterminal body, the anterior part of the hippocampus and the new "general cortex." This suggests a greater functional demand from these regions. The old channel is indicated by the small branches which run anteriorly along the medial border of the palaeo-olfactorium to the olfactory stalk and which suffice for the requirements of these parts. Thus the palaeo-olfactorium retains the old vascular ring which, existing in fishes as the two major arteries—the medial and lateral olfactory arteries—is represented in Reptiles by the middle cerebral artery and small branches of the anterior cerebral artery.

Summary

1. The reptilian brain is still enveloped by a closed primitive vascular network. From this network three major channels—the anterior, middle and posterior cerebral arteries—have become enlarged to carry the bulk of blood in relation to the structures they supply. In addition, an inferior cerebral artery has been described for *Sphenodon* by Dendy.

2. The anterior cerebral artery represents the medial olfactory artery of lower forms. It supplies the medial aspect of the palaeo-olfactorium including the paraterminal body. In addition it reaches the anterior part of the hippocampus and ends in the general anastomosis over the primordium neopallii. The original course of the artery is indicated by a few small branches running forwards along the medial border of the palaeo-olfactorium. The main stream of blood has been deflected to the medial wall of the hemisphere, probably in response to the increased demands made by the expanding paraterminal body and the developing "general cortex."

3. The middle cerebral artery appears as an entity for the first time in Reptiles and has probably developed from the lateral olfactory artery of Fishes through an intermediate ancestral form which has since disappeared. Its representative in Amphibia is the striatal branch of the lateral olfactory artery together with the pyriform branches. The middle cerebral artery supplies the lateral part of the palaeo-olfactorium, the hypopallium and most of the pyriform lobe, and ends in the general anastomosis over the primordium neopallii. .

4. The arteries to the basal ganglia comprise three groups. One enters the pyriform cortex to reach the dorsal fold of the hypopallium, the second enters the rhinal fissure to supply the medial part of the hypopallium and the dorsal parts of the palaeo-striatum and primitive amygdala and the third enters the lateral part of the palaeo-olfactorium to supply the lateral parts of the palaeo-striatum and primitive amygdala.

5. The inferior cerebral artery was described by Dendy as a separate entity in the brain of *Sphenodon*, but does not exist as such in the crocodile. In this animal it is represented by an anastomotic chain between the cranial division of the internal carotid artery and the posterior cerebral artery. The condition found in crocodiles probably represents the reptilian pattern. In *Sphenodon* the inferior cerebral artery is the enlarged anterior part of this anastomotic chain which, nevertheless, is still intact, although its posterior part has remained so small that it is not seen in the injected specimen. The inferior cerebral artery supplies the ventro-medial aspect of the posterior part of the striatum and the ventral part of the primitive amygdala. It also gives a few branches to the posterior part of the pyriform cortex and reaches the posterior part of the medial and lateral fore-brain bundles.

6. The posterior cerebral artery[1] is mainly the hippocampal artery which has acquired a nearer source of origin for its blood by means of a more posterior anastomosis with the cranial division of the internal carotid artery. It supplies nearly all of the hippocampal formation and the posterior part of the paraterminal body. In addition, it supplies the posterior part of the pyriform lobe and primitive amygdala, and joins the common anastomosis over the "general cortex."

7. Finally, each cerebral artery anastomoses at the periphery of its superficial distribution with branches of its fellows and so the primitive vascular net remains intact. The only area over which all three major arteries meet is the newly formed "general cortex."

MAMMALIA

The description of the mammalian cerebral arteries falls into two groups, sub-Primates and Primates. The account of the former group will be based upon the condition found in the sheep, supplemented by reference to other animals where necessary; the condition in Primates will be illustrated by the human pattern as the similarity of the cerebral arteries of apes renders a separate description unnecessary.

SUB-PRIMATES

The great gap between Reptile and Mammal is reflected in the enormous overgrowth of the neopallium which forms a continually enlarging cerebrum in an ascending phylogenetic series. This expansion has caused a secondary deformation of the cerebral hemispheres, so that eventually they appear to have become folded on themselves between the amygdaloid nucleus and foramen of Monro. The palaeo-olfactorium has maintained its original position and the neo-olfactorium has developed around and above it. The primordium neopallii has appeared between the hippocampus and pyriform lobe and by its rapid expansion has pushed these ventrally and then medially so that they come to be relegated to a comparatively insignificant position at the hilum of the brain. Associated with these changes are the appearance of the corpus callosum, the breaking through of the internal capsule and the consolidation of the basal ganglia. Equivalent and comparable alterations have occurred in vascular distribution, but the arteries are the same as in lower forms and, while retaining their old connections and fields of supply, they have contrived to deal adequately with the greatly increased demands made upon them.

When we examine the base of the brain of a primitive Mammal (fig. 5 B and C) we notice that in consequence of the dorso-posterior expansion of the

[1] In a previous paper(9) I have described the posterior cerebral artery of Reptiles as part of the caudal division of the internal carotid artery. This is incorrect because the posterior cerebral artery of Reptiles has no direct relation to the caudal division. It is not until the mammalian stage of evolution is reached that the posterior cerebral artery acquires its connection with the caudal division.

hemisphere, the pyriform lobe becomes bent. This is accompanied by a bending of the rhinal and endorhinal fissures. As we ascend the phylogenetic scale this lateral bend becomes progressively more acute until in Primates the anterior and posterior parts of the endorhinal fissure lie almost parallel. It will simplify the subsequent description if we refer to these parts as the anterior and posterior endorhinal fissures respectively.

In fig. 5 C is shown the base of the brain of a kudu (*S. strepsiceros*) which is sufficiently like that of a sheep to serve for illustration. The internal carotid artery divides alongside the hypophysis into cranial and caudal branches: the cranial division passes anteriorly over the optic tract while the caudal division runs posteriorly to join the basilar artery as before. It will be noticed that the posterior cerebral artery no longer arises from the cranial division. Hofmann has shown how the posterior cerebral artery appears to arise more and more posteriorly as we ascend the phylogenetic scale, these successively posterior positions he has called α, β, γ, and δ. In sub-Mammalia the posterior cerebral artery arises from the cranial division of the internal carotid artery, in Mammalia it receives the bulk of its blood from the basilar artery. At present we can note without comment that the posterior cerebral artery in Mammals appears to arise from the basilar artery.

The posterior cerebral artery runs to the medial surface of the hemisphere where it supplies the general cortex of the posterior parts of the medial, lateral and inferior surfaces, and the posterior pole. Some of the branches to the inferior surface pass forwards to supply the posterior part of the pyriform cortex and anastomose there with the pyriform branches of the middle cerebral and anterior choroidal arteries. As in Reptiles, the posterior cerebral artery supplies most of the hippocampal formation. In true Mammals the growth of the corpus callosum has stretched the antero-superior part of this structure which remains as an attenuated remnant—the supracallosal hippocampus. This survivor represents the part supplied by the anterior cerebral artery in sub-Mammals and so the hippocampal branches of the posterior cerebral artery extend only to the posterior end of the corpus callosum where they anastomose with hippocampal branches of the anterior cerebral artery. In Marsupials where there is no corpus callosum to stretch the paraterminal body and antero-superior part of the hippocampus, the condition approaches that in Reptiles but the hippocampal branches of the posterior cerebral artery do not extend as far anteriorly on the medial wall of the hemisphere as in sub-mammalia. At the antero-inferior part of the hippocampal formation the posterior cerebral branches anastomose with anterior choroidal branches which supply a portion of this formation. The posterior cerebral artery supplies the choroid plexus of the third ventricle and most of that of the lateral ventricle. The posterior cerebral artery usually supplies a small part of the tail of the caudate nucleus. By its stem of origin this vessel also supplies the anterior and superior parts of the mid-brain.

The next artery of importance is the anterior choroidal which takes origin

from the cranial division of the internal carotid artery, now the stem of the internal carotid artery. The artery runs posteriorly along the optic tract and ends by joining the posterior cerebral artery over the lateral geniculate body (9). In its posterior passage (fig. 7) it supplies a small part of the pyriform cortex, the postero-medial aspect of the underlying amygdaloid nucleus and most of the tail of the caudate nucleus. It sends branches to the optic tract, the dorsal nucleus of the lateral geniculate body, the middle third of the crus cerebri and the antero-inferior parts of the hippocampal formation and choroid plexus. Other branches pierce the optic tract to supply the posterior part of the posterior limb of the internal capsule and most of the medial two-thirds of the globus pallidus. A few twigs reach the ventro-lateral nucleus of the thalamus. The anterior choroidal artery anastomoses with the middle and posterior cerebral arteries over the pyriform cortex, with the posterior cerebral artery over the lateral geniculate body and crus cerebri and in the choroid plexus of the lateral ventricle, and with the anterior and middle cerebral and posterior communicating arteries over the anterior part of the optic tract and chiasma (see figs. 7, 10 and 11).

The middle cerebral artery in Mammalia has so enlarged that it appears to be the main trunk of the cranial division (it is often so described in standard text-books) while the anterior cerebral artery—the true anterior continuation—is relatively much smaller. The middle cerebral artery passes laterally in the posterior endorhinal fissure to which it is closely attached as far as the lateral bend; at this spot the main trunk of the vessel passes across the pyriform cortex and rhinal fissure to reach the general cortex laterally and dorsally (fig. 5 C). A small branch, however, runs forwards in the anterior endorhinal fissure to reach the lateral aspect of the olfactory stalk as a reminder of the original course of the artery. The middle cerebral artery supplies most of the pyriform lobe, the antero-lateral aspect of the amygdaloid nucleus, parts of the striatum and most of the lateral aspect of the general cortex.

The striatal branches fall again into three groups: through the pyriform cortex, the endorhinal fissure and the lateral part of the palaeo-olfactorium (fig. 10). Those which pierce the pyriform cortex run into the external capsule and reach the claustrum, and it will be noticed (fig. 5 C) that the majority pass into the groove just lateral to the lateral olfactory tract and its nucleus. They were described for *Echidna* by Shellshear (7), who follows the description of Sonntag and Woollard for *Orycteropus* (32) and calls the endorhinal fissure the arcuate fissure and the fissure lateral to the nucleus of the lateral olfactory tract the endorhinal fissure. (This information I obtained in a personal communication from Prof. Shellshear who agrees with my interpretation of this region.) The lateral striate arteries proper enter the endorhinal fissure and pass to the external capsule between the claustrum and putamen. They then enter the putamen and, passing dorsally through it, cross the superior part of the internal capsule to end in the caudate nucleus (fig. 7). Anteriorly, these arteries supply the dorso-lateral part of the head of the caudate-putamen

mass and the upper part of the anterior limb of the internal capsule; more posteriorly they pass through the putamen and across the upper part of the posterior limb of the internal capsule to reach the body of the caudate nucleus. The striatal branches through the palaeo-olfactorium supply the lateral part of the globus pallidus and amygdaloid nucleus. The majority of the branches to the amygdaloid nucleus pass through the pyriform cortex and endorhinal fissure.

The small continuation of the middle cerebral artery in the anterior endorhinal fissure supplies striatal branches, branches to the pyriform cortex and

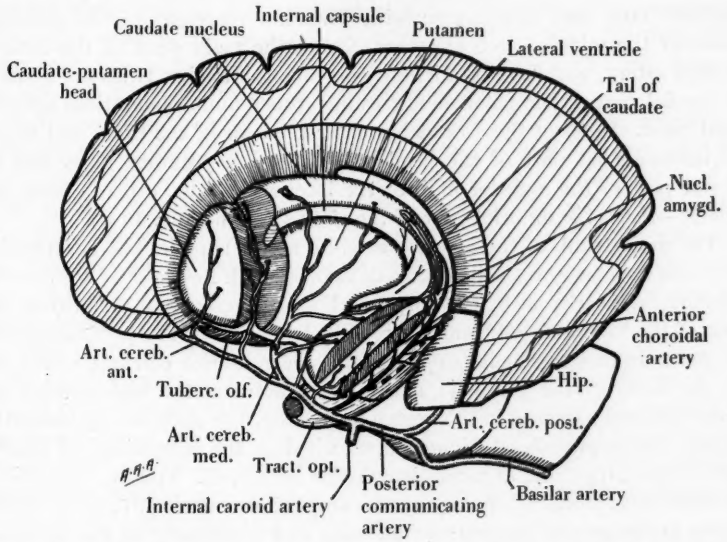

Fig. 7. Brain of sheep, dissection of the basal ganglia and their arteries from the lateral aspect. The amygdaloid nucleus has been cut in steps to show its double blood supply, and a section has been cut from the caudate-putamen head to show the distribution of an anterior cerebral branch. Anterior choroidal artery in black. Note branch of anterior choroidal artery in tail of caudate nucleus, and in posterior limb of internal capsule.

palaeo-olfactorium, and anastomotic branches to the anterior cerebral artery over the palaeo-olfactorium, and finally passes on to the lateral aspect of the olfactory bulb where it ends by joining more anterior cerebral branches. Thus the stem of middle cerebral artery in the posterior endorhinal fissure, and the small branch in the anterior endorhinal fissure together represent nearly all of the middle cerebral artery of Reptiles and preserve its distribution and relations exactly. The rest of the artery in Mammals has developed from the common anastomosis in relation to the growing neopallium.

The anterior cerebral artery is the forward continuation of the cranial division of the internal carotid artery. From its point of origin (fig. 5 C) it

passes forwards and then medially to the medial border of the palaeo-olfactorium where it usually joins its fellow of the opposite side. Thence the combined vessel ascends over the front of the corpus callosum where it divides again into its components which run posteriorly over the dorsum to anastomose finally with hippocampal branches of the posterior cerebral artery. This is merely an extension of the course of the homologous vessel of the Reptile due to the stretching of the anterior part of the hippocampal formation by the growing corpus callosum. As in the Reptile, the primitive course of the anterior cerebral artery along the medial border of the palaeo-olfactorium is maintained by some small branches which reach the medial aspect of the olfactory bulb and anastomose with branches representing the primitive course of the middle cerebral artery. From the main stem of the anterior cerebral artery, and from its forward continuing branches twigs are given to the medial part of the palaeo-olfactorium—tuberculum olfactorium and diagonal band. Many of these branches enter the base of the brain and supply the infero-medial part of the head of the caudate-putamen mass and the inferior part of the anterior limb or the internal capsule, others—more posteriorly—reach the anterior part of the globus pallidus (fig. 10 B).

The main trunk of the anterior cerebral artery supplies the paraterminal body and the structures which have developed with it—most of the anterior commissure, nearly all of the corpus callosum, the septum pellucidum and most of the hippocampal commissure (Elliot Smith (33)). The posterior part of the paraterminal region is supplied from the posterior cerebral artery and the survivors of the primitive anastomoses between the hippocampal and medial olfactory arteries in this region in the frog. The anterior cerebral artery supplies the supracallosal hippocampus which is the morphological anterior part of the hippocampal formation (Elliot Smith (34)). Finally, branches of the anterior cerebral artery supply the neopallium anterior to and above the corpus callosum and anastomose laterally and posteriorly at the periphery of their field of distribution with branches of the middle and posterior cerebral arteries respectively.

The homologies of these arteries are clear, but the posterior cerebral artery merits closer attention. This vessel arises from the basilar artery in Mammals and supplies much of the anterior part of the mid-brain. From the posterior cerebral artery a number of small branches pass to the anterior part of the temporal region (which is morphologically the posterior pole of the pyriform lobe) and join pyriform branches of the cranial division—from the stem of the carotid artery and the middle cerebral artery—some of which represent the stem of the reptilian posterior cerebral artery. Frequently these twigs receive their blood from the anterior choroidal artery and constitute the pyriform branches of this vessel, their true nature is thus often obscured but such vessels are always present and show the way by which the posterior cerebral artery has passed.

The posterior communicating artery runs from the internal carotid artery

to the basilar and is clearly the caudal division of the internal carotid. Branches of this vessel join the anterior choroidal in a rich anastomosis over the optic tract and thus may supply indirectly some of the anterior choroidal field. These communications are usually slight, and the amount of blood they convey negligible, but cases have been described by Kolisko (35) and others, and I have seen one such, where the anterior choroidal is minute or even represented by a series of tiny twigs. Under these circumstances the posterior communicating artery enlarges and takes over nearly the whole of the field of the anterior choroidal artery. On the other hand the posterior communicating artery may be very small; in this case the anterior choroidal artery shows a compensatory enlargement. Sometimes, when the communication with the basilar artery is small and the posterior communicating artery diminished, the posterior cerebral artery receives most of its blood from the anterior choroidal channel which thus forms its stem.

Hofmann calls the lateral olfactory artery of Amphibia the *arteria cerebralis posterior* α; this has been discussed. He also calls the anterior choroidal artery of Mammals the *arteria cerebralis posterior* α and is justified in so far as the anterior choroidal artery arises from the cranial division of the internal carotid artery and occasionally forms the stem of the posterior cerebral artery. But, as I have shown elsewhere (9), the anterior choroidal artery is the homologue of the inferior cerebral artery of *Sphenodon* plus its anastomotic connection with the posterior cerebral artery and its more recently acquired choroidal branches. When it acts as the stem of the posterior cerebral artery of Mammals it does so not because it is reassuming an old function, but because other factors have come into play. The true primitive stem of the posterior cerebral artery exists among the small anastomotic channels over the posterior part of the pyriform lobe. That these often receive their blood through the anterior choroidal artery is to be regarded as another example of the principle of economy of distribution.

In Mammalia the posterior cerebral artery is said to arise from the basilar artery. What is really implied is that it receives its main contribution of blood through the basilar artery. The main trunk of the posterior cerebral artery supplies the anterior part of the mid-brain. Frequently some of its mid-brain distribution is undertaken by smaller vessels which may remain discrete at their origin from the basilar artery or may arise from a common stem with the posterior cerebral artery to separate later. In an ascending phylogenetic scale these separate mid-brain vessels become progressively less frequent, they are commonly found in lower Mammals, less often in higher. As the cerebral hemispheres become pushed backwards over the mid-brain the distribution of the posterior cerebral artery becomes separated more and more from its source of supply. Consequently it appears to shift its stem of origin posteriorly as successively posterior anastomotic channels enlarge to carry the main stream of blood from a nearer source. Thus the posterior cerebral artery grows so far away from its primitive parent—the internal

carotid artery—that even the caudal division will not suffice for its requirements. It takes more and more of its blood from the nearest large vessel—the basilar artery—and this it does through anastomotic channels with mid-brain vessels, while the basilar artery itself enlarges to meet the increased demands. Sometimes the internal carotid artery exerts its old influence and supplies the posterior cerebral artery through the posterior communicating or anterior choroidal channels, but such cases are rare and but repetitions of primitive patterns. When the posterior cerebral, or any other artery, employs as its medium of supply a vessel which has its own definite field of distribution the common trunk serves to provide both areas and the larger vessel appears to absorb the smaller. The posterior cerebral artery of higher Mammals uses the anterior mid-brain arteries as its nearest source of blood and gives the impression that the posterior cerebral artery is an artery of the anterior part of the mid-brain.

Hofmann's classification of the posterior cerebral artery in terms of its points of origin is justified, but it must be emphasised that these are not new vessels. The channels have always existed in the primitive network which envelopes the brain. As the posterior cerebral artery has grown away from its old source the next posterior channel has enlarged to carry the main flow of blood; when this is discarded to give place to a yet more posterior source it does not disappear but reverts to its original state as a small anastomotic channel in the primitive network, and should circumstances demand, it will again enlarge to carry out its old function.

The stem of the middle cerebral artery is the same in origin and course as its predecessor in the Reptile, and the first part of its trunk which is so closely related to the posterior endorhinal fissure has only altered in size. Thereafter the character of the vessel changes completely. In reptiles the main course of the artery is along the endorhinal fissure to the olfactory stalk, while the pyriform branches are of subsidiary importance; in Mammals the main trunk of the artery leaves the endorhinal fissure at its lateral angle and traverses the pyriform lobe to reach the neopallium. The old main vessel is represented by a small branch which runs in the anterior endorhinal fissure to reach the olfactory bulb (fig. 5 C). This small vessel, however, suffices for the needs of all the structures supplied by this part of the original middle cerebral artery. The call for extra blood has come from the growing neopallium and has been met by an enlargement of the pyriform branches which now cross the pyriform cortex and rhinal fissure to supply the general cortex. The new main flow of blood is through the stem and pyriform branches of the middle cerebral artery but the old channel in the anterior endorhinal fissure, having little or no extra demand to meet, persists comparatively unchanged.

The anterior cerebral artery, although much larger, pursues the same course as in Reptiles. Its greatest flow of blood is to the medial wall of the hemisphere to supply the expanding paraterminal body and general cortex. The original course and distribution are served through the small branches which

run forwards along the medial border of the palaeo-olfactorium to the olfactory bulb.

Thus, in Mammals the enormous growth of the neopallium has made use of the old stem arteries for its supply of blood, but the cortical arteries have developed from the common anastomosis of the three major vessels over the primordium neopallii of Reptiles. No new arteries have been formed, the demand has been satisfied by the enlargement of existing arterial channels. The palaeo-olfactorium of the dogfish was so important that it formed a very large part of the hemisphere and the blood supply of this primitive brain encircled, and was evolved almost entirely for that structure. In Mammalia the palaeo-olfactorium is small and hidden at the base of the brain; it has changed little from its primitive condition and retains the arterial circle in its original state. Although the vessels of this circle are as large as, or even larger than, those of the original circle, they are diminutive in comparison with the other cerebral arteries. The demands of the neopallium have been more urgent and imperative.

The question of the evolution of the basal ganglia is difficult and controversial, but it is hoped that the study of the arterial supply may contribute towards its solution. If arteries are constant in their terminal supply it should be possible to trace homologous structures from sub-Mammals to Mammals.

The anterior cerebral artery supplies the medial and anterior part of the palaeo-striatum in *Sphenodon* (fig. 6); the homologous vessel in mammals supplies the infero-medial part of the head of the caudate-putamen mass and the anterior part of the medial two-thirds of the globus pallidus (fig. 10). It appears that inferior part of the caudate-putamen mass and this part of the globus pallidus have evolved from the antero-medial part of the palaeo-striatum.

The middle cerebral artery supplies the whole of the hypopallium and the dorso-lateral parts of the palaeo-striatum and primitive amygdala of sub-Mammals; in Mammals it reaches the supero-lateral part of the head of the caudate-putamen mass, the claustrum, the putamen and the body of the caudate nucleus, the antero-lateral aspect of the amygdaloid nucleus and the lateral one-third of the globus pallidus (fig. 10). Further, it was observed that the striatal branches formed three groups; through the pyriform cortex to the dorsal fold of the hypopallium, through the endorhinal fissure to the medial fold of the hypopallium and the dorsal part of the palaeo-striatum and primitive amygdala and through the lateral part of the palaeo-olfactorium to the lateral part of the palaeo-striatum. These groups are as distinct in the mammalian brain. The vessels through the pyriform cortex supply the claustrum, those through the endorhinal fissure the putamen and the body of the caudate nucleus as well as the dorso-lateral part of the head of the caudate-putamen mass and the lateral part of the globus pallidus and amygdaloid nucleus, those through the palaeo-olfactorium the intermediate parts of the globus pallidus and amygdaloid nucleus.

The anterior choroidal artery is represented in *Sphenodon* by the inferior cerebral artery and its anastomotic union with the posterior cerebral artery. In Mammals it acquires choroidal branches from the posterior cerebral artery. The inferior cerebral artery supplies the ventro-medial part of the primitive amygdala and of the posterior part of the palaeo-striatum (that is, all of this which is not supplied by the anterior and middle cerebral arteries). In Mammals the anterior choroidal artery supplies the postero-medial part of the amygdaloid nucleus and the posterior portion of the medial two-thirds of the globus pallidus as well as most of the tail of the caudate nucleus (see fig. 7). The rest of the tail is supplied by the posterior cerebral artery.

In fig. 11 I have tried to show diagrammatically the evolution of the basal mass and its arteries. In *Sphenodon* there is a conglomerate mass formed by the accretion of the separate primordia of the frog. With the expansion of the neopallium the dorsal hypopallium is pushed laterally and ventrally and comes to lie dorsal and lateral to the palaeo-striatum. At the same time the internal capsule has broken through the basal mass along the broken heavy line indicated in the *Sphenodon*. This it does without regard to individual cell masses as Johnston showed (18). Thus it separates the hypopallial fold in its dorsal and ventral parts giving rise to the body of the caudate nucleus which is almost completely cut off from the more ventral claustrum and putamen. Johnston has emphasised (p. 358) that the separation by the internal capsular fibres is incomplete, and that the caudate nucleus and putamen are connected in the upper part of the internal capsule by strands of cells which are continuous with both structures and indistinguishable from the cells of either. Anteriorly the separation is even less complete, the head of the caudate-putamen mass is broken through by the fibres of the anterior limb of the internal capsule but the strands of cells which persist between the bundles of fibres are so thick that they impart the striated appearance to which the body owes its name. Anteriorly, too, the medial and lateral masses of cells are continuous below the anterior limb of the internal capsule (fig. 10). Posteriorly, the break is again incomplete. It extends down into the primitive amygdala and splits off incompletely the posterior part of this body in such a way that this split-off part retains its connection below the posterior limb of the internal capsule with the parent cell mass. Superiorly it is continuous with the posterior end of the body of the caudate nucleus. This split-off portion of the primitive amygdala constitutes the tail of the caudate nucleus and retains the blood supply of the parent mass from the anterior choroidal and posterior cerebral arteries. In *Notoryctes typhlops* the cells of the amygdaloid nucleus are continuous with, and indistinguishable from, those of the tail of the caudate nucleus, nor can one tell where one gives place to the other. (Miss Fielding of this department kindly drew my attention to this circumstance.)

After the separation of the anterior, dorsal and posterior elements of the basal ganglia there remains undisturbed the larger part of the mass. This is composed of many cell groups. Anteriorly and lateral to the anterior limb is

the outer part of the head of the caudate-putamen mass comprising palaeo-striatum ventrally and some of the hypopallium dorsally. These are continued posteriorly into the main part of the lenticular nucleus which has globus pallidus (palaeo-striatum) medially and putamen (hypopallium) laterally. The putamen is continuous with the hypopallial part of the amygdaloid nucleus ventrally and the globus pallidus with the primitive amygdala (fig. 10).

Thus, it appears that the hypopallium has formed the claustrum from its dorsal fold and the body and part of the head of the caudate nucleus and the putamen from its most medial part. The posterior part of the hypopallium has formed the antero-lateral part of the amygdaloid nucleus. The primitive amygdala has evolved into the postero-medial part of the amygdaloid nucleus and the tail of the caudate nucleus, the palaeo-striatum into the globus pallidus and the infero-medial part of the head of the caudate-putamen mass. The arteries have maintained their field of supply constantly from sub-Mammal to Mammal.

In *Sphenodon* the inferior cerebral artery supplies the lower part of the lateral fore-brain bundle posteriorly and the anterior cerebral artery the anterior part. The middle cerebral artery supplies the upper part of the whole bundle. The blood supply of the internal capsule of Mammals corresponds. The anterior choroidal artery supplies the posterior part of the internal capsule to the upper level of the globus pallidus and the anterior cerebral artery the ventral part of the anterior limb; the middle cerebral artery supplies the dorsal parts of both limbs. There is little or no infralenticular development of the internal capsule in sub-Mammalia (fig. 7).

Summary

1. The brain of the sub-Primates retains the primitive arterial network intact. Within this the various arteries have enlarged to meet the demands of the growing neopallium.

2. The cerebral arteries have retained their old stems of origin and are named as in Reptiles the anterior, middle and posterior cerebral arteries. The enlargement has been provided from the common anastomosis over the primordium neopallii.

3. The anterior cerebral artery is very little changed in origin and course, it passes to the medial wall of the hemisphere to supply the paraterminal body and antero-superior part of the hippocampus (now supracallosal hippocampus) and its share of the neopallium. Its primitive course is followed by small branches which run along the medial border of the palaeo-olfactorium to the olfactory stalk and supply the medial parts of both.

4. The middle cerebral artery arises from the stem of the internal carotid artery and runs in the posterior endorhinal fissure as usual. At the lateral angle of the fissure the main channel crosses the pyriform lobe to reach the lateral aspect of the neopallium most of which it supplies. Small branches in

the anterior endorhinal fissure follow the old course to the olfactory bulb and supply the lateral parts of the palaeo-olfactorium and bulb. The palaeo-olfactorium thus retains its arterial circle, but this is relatively much diminished in size.

5. The striate branches of the middle cerebral artery again fall into three groups. One through the pyriform cortex to the claustrum, one through the endorhinal fissure to the putamen, the body of the caudate nucleus, the lateral part of the globus pallidus and the lateral part of the amygdaloid nucleus and one through the lateral part of the palaeo-olfactorium to the intermediate parts of the globus pallidus and amygdaloid nucleus. It is considered that these are homologous with the similar arteries of Reptiles.

6. The anterior choroidal artery has developed from the inferior cerebral artery of *Sphenodon* and its anastomosis with the posterior cerebral artery. In Mammals this vessel acquires some choroidal branches from the posterior cerebral artery to the antero-inferior part of the choroid plexus. Of the basal ganglia it supplies the postero-medial part of the amygdaloid nucleus, most of the tail of the caudate nucleus and most of the globus pallidus. It is considered that the tail of the caudate nucleus is the split-off posterior part of the primitive amygdala.

7. The posterior cerebral artery has had its field of supply moved posteriorly with the dorso-posterior expansion of the hemisphere. As a consequence, the vessel has shifted its stem posteriorly to maintain its blood supply from the nearest source. This it has done by employing successively posterior stems of origin. Eventually the posterior cerebral artery has come to receive its blood from anterior mid-brain channels which enlarge to carry the increased volume of blood. At the same time the basilar artery has enlarged to supply this greater volume of blood and the posterior cerebral artery appears to arise directly from the basilar. The successive stems of origin used are existing anastomotic channels from the primitive network, they revert to their former state when no longer required.

8. The posterior cerebral artery supplies most of the hippocampus, the posterior parts of the inferior, medial and lateral surfaces of the hemisphere, a small portion of the tail of the caudate nucleus and the anterior part of the mid-brain. The supply to the tail of the caudate nucleus corresponds with the supply from the homologous vessel to the posterior part of the primitive amygdala of Reptiles.

9. The cerebral arteries all anastomose at the periphery of their superficial fields of supply and maintain the primitive vascular network.

10. The evidence of the blood supply supports the view that the hypopallium has given rise to the claustrum, putamen, body and some of the head of the caudate nucleus and the antero-lateral part of the amygdaloid nucleus. The palaeo-striatum has formed the ventro-medial part of the head of the caudate-putamen mass and the globus pallidus; the primitive amygdala the

postero-medial part of the amygdaloid nucleus and the tail of the caudate nucleus.

PRIMATES

The cerebral arteries were examined in lemurs, apes and Man. Except in the case of the lemur whose vessels were somewhat anomalous, the arteries were so similar that the description of one will suffice. Change in the brain in the passage from sub-Primates to Man is of degree only. In the acquisition of the neopallium and corpus callosum the Mammals had accomplished their most difficult task and further alteration is expressed in the growing dominance of these structures. The arteries show little difference. Their pattern, course and distribution habits have become fixed and, but for the increased supply to the enlarged neopallium, they are the same. The cerebral hemispheres in Man have carried the dorso-posterior expansion to an extreme degree. The mid-brain is entirely hidden and the bending of the pyriform lobe is so acute that its angle is buried with the insula. The corpus callosum has stretched the supracallosal hippocampus to an attenuated remnant, the cavum septi is closed in front, the internal capsular fibres have increased enormously and the tail of the caudate nucleus is drawn out to a thin band. The palaeo- and neo-olfactoria have been thrust away to the basal and medial surfaces of the hemisphere. These structures are still present, however, and despite the dominance of the neopallium, they demand and receive the same blood supply as they have always enjoyed.

The forebrain arteries of Man have been studied extensively by many workers—Duret (12), Heubner (36), Kolisko (35), Beevor (37), Aitken (38), and Shellshear (6). The majority have been content to describe what they found together with variations from what they considered to be the normal. Shellshear, alone, has tried to correlate evolutionary changes in the brains of apes and Man with the morphology of the arteries. He has dealt thoroughly with the cortical distribution of the arteries and his correlation can be extended with advantage to non-cortical areas.

The posterior cerebral artery has reached its ultimate posterior stem of origin, its field of supply lies almost directly over the mid-brain and it employs exclusively mid-brain vessels for its source of blood. Even in Man, however, some of the arteries to the anterior part of the mid-brain may arise separately from the basilar artery. More frequently they come from the posterior cerebral stem close to its origin. In Man, too, cases have been reported where the posterior cerebral artery obtained most of its blood from the internal carotid artery through the posterior communicating or anterior choroidal arteries. Such examples indicate the route by which the origin of the posterior cerebral artery has travelled backwards. The distribution of this vessel is in all ways comparable with that of lower Mammals: the posterior part of the general cortex and pyriform lobe, most of the hippocampal formation and choroid plexus of the third and lateral ventricles and a small part of the tail of the caudate nucleus. It anastomoses with the anterior cerebral artery over

the posterior part of the supracallosal hippocampus and general cortex of the dorso-medial wall of the hemisphere, with the middle cerebral artery over the posterior part of the pyriform cortex and the temporal and occipital lobes and with the anterior choroidal artery over the pyriform cortex, the lateral geniculate body and antero-inferior parts of the hippocampal formation and in the choroid plexus of the lateral ventricle.

The anterior choroidal artery, with the elongation of the choroidal fissure, has acquired more choroidal branches but is otherwise little changed. It supplies some of the pyriform cortex, the postero-medial part of the amygda-

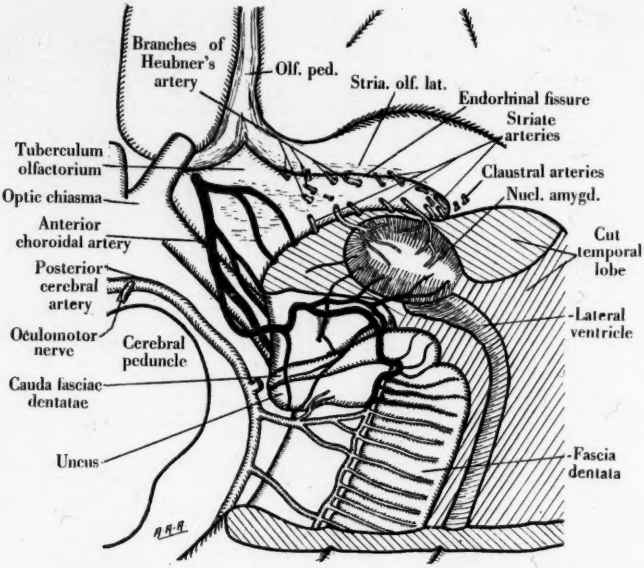

Fig. 8. Human brain dissected from the base to show the distribution of the striatal branches through the anterior perforated space and endorhinal fissure. This shows also the double blood supply to the amygdaloid nucleus and the distribution of the arteries to the uncus and fascia dentata. Anterior choroidal artery black.

loid nucleus, the uncus and the antero-inferior part of the hippocampal formation. It sends branches to the posterior two-thirds of the optic tract and the lateral part of the lateral geniculate body, the middle third of the crus, most of the tail of the caudate nucleus and the antero-inferior part of the choroid plexus of the lateral ventricle. Perforating vessels pass to the upper parts of the red nucleus and substantia nigra, frequently to the ventro-lateral nucleus of the thalamus and to the corpus subthalamicum. Others reach the beginning of the optic radiation, most of the medial part of the globus pallidus and the posterior two-thirds of the posterior limb of the internal capsule to the upper level of the globus pallidus (figs. 8, 9 and 10).

The middle cerebral artery supplies most of the area involved in the recent development of the cortex and shows some important changes. The bending of the endorhinal fissure has caused the anterior and posterior endorhinal fissures to lie almost parallel (fig. 5 D). The main trunk of the middle cerebral artery arises from the stem of the internal carotid artery and runs in the posterior endorhinal fissure. Over the limen insulae the artery leaves the fissure and crosses the pyriform lobe to reach the general cortex as in sub-Primates. The small branches in the anterior endorhinal fissure show the greatest changes. These branches dwindle as they pass medially away from their source of blood and as they approach the anterior cerebral artery the anastomoses with this vessel enlarge to supply the added field. Thus the anterior cerebral artery comes to supply regions which rightfully belong to the middle cerebral. This usurpation occurs chiefly in the most medial (morphologically anterior) part of the endorhinal fissure and the striate vessels in this region receive their blood from the anterior cerebral artery. The anterior cerebral artery also takes over the supply of some of the originally lateral part of the palaeo-olfactorium.

Other changes are apparent in this region. With the approximation of the anterior and posterior endorhinal fissures the anastomoses over and around the palaeo-olfactorium become crowded and there are too many for their requirements. One large channel will suffice and only one anastomosis is retained at the original standard. The remainder dwindle, but persist as tiny anastomotic channels which are never described. The single large vessel obtains nearly all of its blood from the anterior cerebral artery and the connection with the middle cerebral is reduced to a rudiment. The artery is usually referred to as the artery of Heubner, but Shellshear (4) has called it the anterior recurrent cerebral artery. Shellshear, too, has described its connection with the middle cerebral artery (see fig. 5 A–D).

Heubner's artery is the survivor of a series of anastomotic channels over and around the palaeo-olfactorium—the most primitive cerebral vascular system—and varies greatly in origin and course. Variations in origin depend upon which anastomotic channel—anterior, middle or posterior—is used as the stem of origin, and the vessel may arise early or late from the anterior cerebral artery. Variations in course depend upon which particular channel is picked out from the network over the palaeo-olfactorium, and the artery may cross this anteriorly or posteriorly or in an intermediate position, or through a trunk which has been derived from parts of all. Whatever its origin and course, the artery of Heubner always supplies the anterior cerebral field, and variations of its total area of distribution depend upon how much of the middle cerebral field it has taken over and how much has been left for the middle cerebral itself to supply.

The middle cerebral artery has been pulled away from its primitive anterior field of supply, and this field included the lateral part of the olfactory bulb. Again the anterior cerebral artery performs its vicarious function and takes

over this area and in Primates it supplies not only both sides of the olfactory bulb but also spreads out laterally to reach the medial part of the orbital surface of the frontal lobe (fig. 5 D). Thus the anterior recurrent cerebral artery affords one of the best examples of the principles of economy of distribution and convenience of source. Since there were too many arteries in this

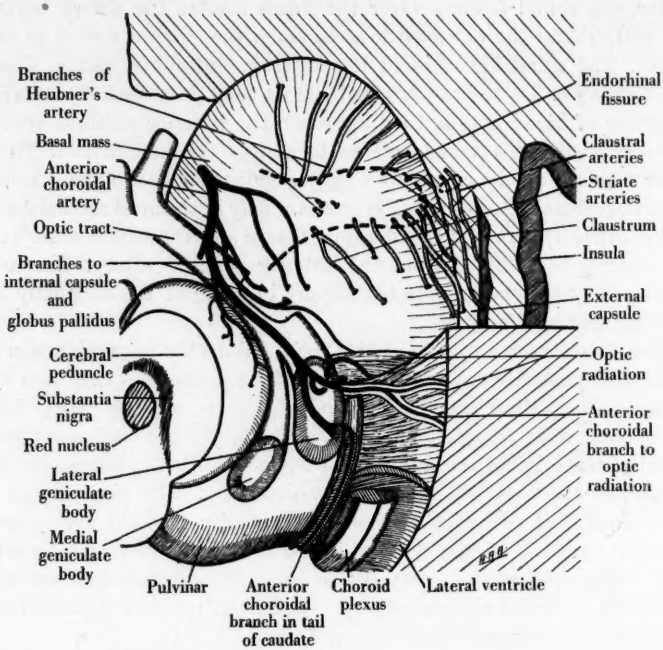

Fig. 9. Human brain, dissection from the base leaving the striatum and its arteries intact. The amygdaloid nucleus has been removed and the position of the endorhinal fissure is indicated by the broken heavy line. A segment has been removed from the optic tract to show how branches of the anterior choroidal artery reach the posterior limb of the internal capsule and the globus pallidus; a branch of the same artery has been dissected in the tail of the caudate nucleus, and the roof of the inferior horn of the lateral ventricle has been partly removed to show how branches of the anterior choroidal artery supply the first part of the optic radiation. Note that the claustral arteries do not pierce the endorhinal fissure but pass through the pyriform cortex to reach the external capsule. Anterior choroidal artery black.

region one was kept to act for all; because the field of supply was pushed away from the middle cerebral artery towards the anterior cerebral this vessel has taken over the supply. No new vessels have appeared and none has been lost. Some channels have enlarged and others dwindled but they are the anastomotic vessels that have always been present. The terminal arterioles are the same whether they receive their blood from the anterior or from the middle cerebral artery.

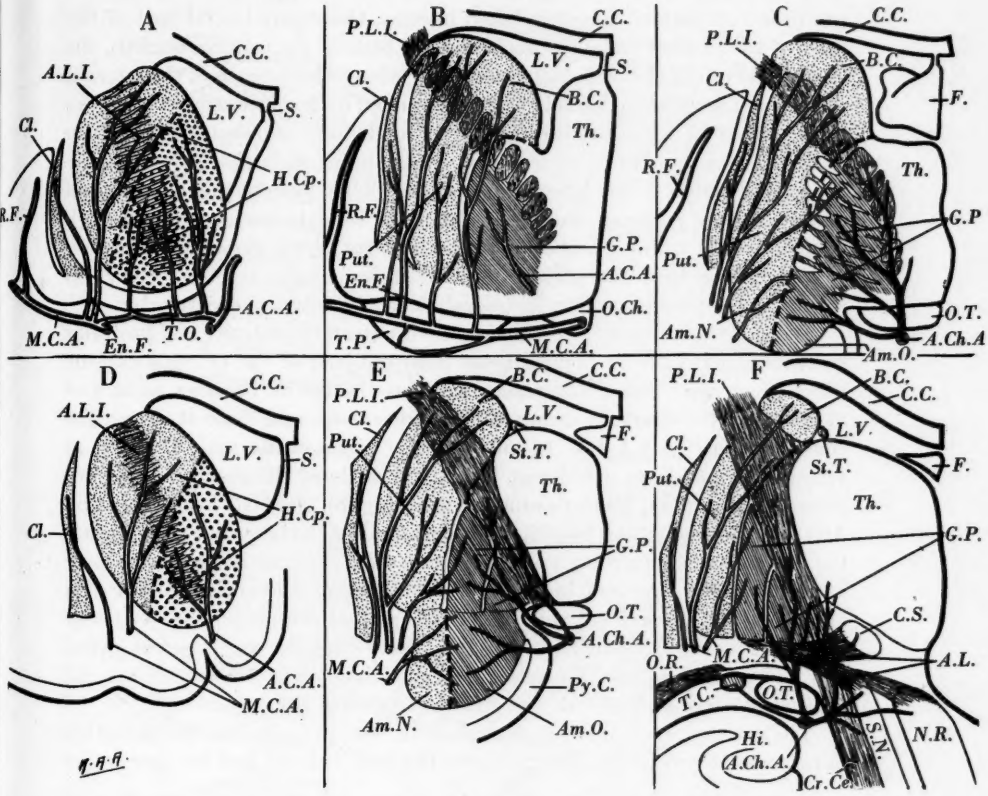

Fig. 10. A series of sections through the basal ganglia of an ungulate (*R. tarandus*, A. B, C) and of a human brain (D, E, F) showing the relation of the arteries. Hypopallium—stippled; palaeo-striatal part of head of caudate-putamen mass—large dots; old amygdala and globus pallidus—oblique lines. Note the three groups of striate branches from the middle cerebral artery and how the most medial of these reach the lateral part of the palaeo-striatum, a branch of the anterior cerebral artery to the globus pallidus (B) and the continuity of the putamen with the new amygdala and the globus pallidus with the old amygdala. The break through of the internal capsule is less complete in the reindeer than in Man. Anterior choroidal artery depicted in black. (Semi-schematic, but based on a large number of sections and dissections of both brains.)

A.C.A. anterior cerebral artery; *A.Ch.A.* anterior choroidal artery; *A.L.* ansa lenticularis; *A.L.I.* anterior limb of internal capsule; *Am.N.* new amygdala; *Am.O.* old amygdala; *B.C.* body of caudate; *C.C.* corpus callosum; *C.S.* corpus subthalamicum; *Cl.* claustrum; *Cr.Ce.* crus cerebri; *En.F.* endorhinal fissure; *F.* fornix; *G.P.* globus pallidus; *H.Cp.* caudate-putamen head; *Hi.* hippocampus; *L.V.* lateral ventricle; *M.C.A.* middle cerebral artery; *N.R.* red nucleus; *O.Ch.* optic chiasma; *O.R.* optic radiation; *O.T.* optic tract; *P.L.I.* posterior limb of internal capsule; *Put.* putamen; *Py.C.* pyriform cortex; *R.F.* rhinal fissure; *S.* Septum; *S.N.* substantia nigra; *St.T.* stria terminalis; *T.C.* tail of caudate; *Th.* thalamus; *T.O.* tuberculum olfactorium; *T.P.* temporal pole.

The middle cerebral artery supplies most of the pyriform lobe and the antero-lateral part of the amygdaloid nucleus, the supero-lateral part of the head of the caudate-putamen mass and the body of the caudate nucleus, the lateral part of the globus pallidus, the upper parts of both limbs of the internal capsule and most of the lateral part of the general cortex. The striatal branches are arranged in the same three groups as in Reptiles: through the pyriform cortex to the claustrum (as was also shown by Shellshear (3)), through the endorhinal fissure to the lateral parts of the globus pallidus and amygdaloid nucleus, to the putamen and the body of the caudate nucleus and through the palaeo-olfactorium to the intermediate parts of the globus pallidus and amygdaloid nucleus. The only change is that the anterior cerebral artery has come to supply the most medial (morphologically anterior) striate arteries.

With the bending of the endorhinal fissure the most anterior and posterior extremities have become pulled away from the base of the external capsule which they must eventually reach; thus, as the fissure becomes more and more flexed, the striate branches at the angle enlarge and those at the medial ends dwindle (fig. 5 A–D). In an ascending phylogenetic scale there is an accumulation of large arteries at the lateral angle of the fissure and a progressively dwindling series passing medially (fig. 8). This has been shown by Aitken, Elliot Smith and Shellshear (3), Duret called the largest of these vessels the lenticulo-striate artery and Charcot showed (39) that it was the artery most frequently involved in cerebral haemorrhage. The concentration of a great number of arteries at the base of the external capsule (fig. 9)—a greater number than in any other part of the brain—explains why Charcot called this the site of election for cerebral haemorrhage. The chances of arterial rupture here are at least twice as great as anywhere else.

The anterior cerebral artery presents little change apart from the reduction in palaeo-olfactory anastomoses to form Heubner's artery, and the usurpation

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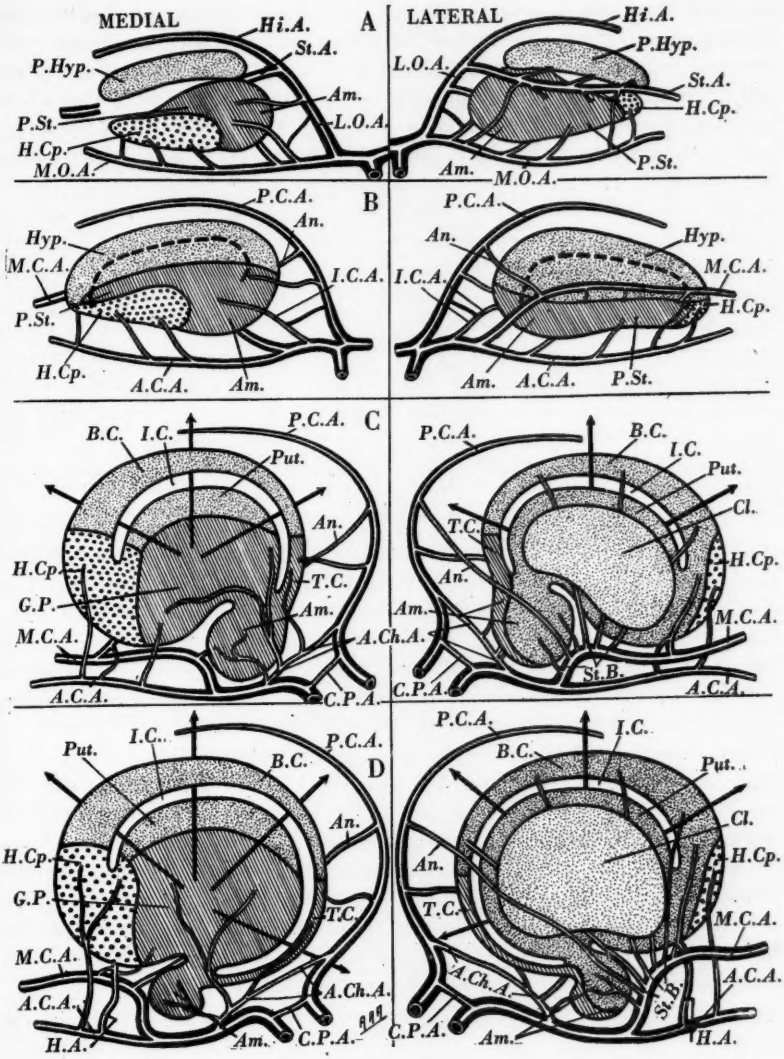
Legend to Fig. 11

Fig. 11. Schema to illustrate the formation of the human striatum. A, amphibian, with the palaeo-striatum well differentiated and the primordium hypopallii (*P. Hyp.*) loosely applied, the arteries as in fig. 3. B, *Sphenodon*, the basal mass well compacted and the arteries differentiated, the broken thick line indicates the region of break through of the internal capsule. C, lower Mammal, the arrows indicate the direction of the capsular fibres, note that the tail of the caudate nucleus is the split-off posterior part of the old amygdala and retains its original blood supply, also the continuity of the new amygdala with the putamen and how the striatal branches pass between the claustrum and putamen to reach the body of the caudate. D, Primate, the dorso-posterior expansion of the hemisphere has drawn the tail of the caudate nucleus in the same direction, and the increase in capsular fibres has accentuated the separation of the caudate from the rest of the basal mass. In particular note the formation of an infralenticular portion of the internal capsule.

Hypopallium—stippled finely; palaeo-striatum and old amygdala—oblique lines; palaeo-striatal part of head of caudate-putamen mass—large dots; *Am.* amygdaloid nucleus; *An.* anastomosis over the pyriform lobe between the middle and posterior cerebral arteries; *C.P.A.* posterior communicating artery; *I.C.* internal capsule; *L.O.A.* lateral olfactory artery. Remaining letters as in previous diagrams.


MEDIAL
A
Hi.A.
St.A.
P.Hyp.
Am.
P.St.
L.O.A.
H.Cp.
M.O.A.
LATERAL
Hi.A.
P.Hyp.
L.O.A.
St.A.
H.Cp.
P.St.
Am.
M.O.A.
B
P.C.A.
An.
Hyp.
M.C.A.
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Am.
C
B.C.
I.C.
Put.
An.
H.Cp.
T.C.
G.P.
Am.
M.C.A.
A.Ch.A.
A.C.A.
C.P.A.
D
Cl.
St.B.

Fig. 11.

of part of the territory of the middle cerebral artery. The vessel forms the anterior continuation of the cranial division of the internal carotid artery as in lower Mammals and is distributed in a comparable manner. The main trunk passes to the medial wall of the hemisphere where it supplies the para-terminal region containing the three great commissures and the septum pellucidum, the supracallosal hippocampal vestiges, the general cortex of the anterior two-thirds of the medial wall of the hemisphere and of the upper part of the lateral wall to about the same extent. (For a detailed account of the cortical distribution of the various cerebral arteries see Shellshear's papers on the orang, chimpanzee and Man.) The primitive course of the anterior cerebral artery is again represented by small branches which run anteriorly along the medial border of the palaeo-olfactorium. These supply the anterior part of the globus pallidus and the infero-medial part of the head of the caudate-putamen mass as well as the inferior half or so of the anterior limb of the internal capsule (fig. 10). The branches also supply the medial parts of the tuberculum olfactorium and olfactory bulb and the medial orbital border and (in consequence of the adoption of some of the middle cerebral field) the lateral part of the olfactory bulb, some of the orbital surface of the frontal lobe lateral to the bulb and a varying amount of the anterior part of the striatum.

Shellshear has shown that the three major arteries always anastomose at the periphery of their cortical fields of supply. His lines of vascular demarcation are too well known to require further discussion. To this may be added that there is no such thing as a non-anastomotic artery on the surface of the brain although the anastomoses are not always sufficiently large to compensate for occlusion of some of them. Every vessel joins another and the primitive network whence they have all arisen remains intact. No cerebral artery becomes an end-artery until it has entered the brain substance, but once within the brain no artery appears ever to join another. When it enters the brain its distribution is fixed and it proceeds alone to the destination which has been its own ever since that part of the brain first appeared. There is no evidence to support Kolisko's statement that the middle cerebral, anterior choroidal and posterior communicating arteries anastomose in the upper part of the genu of the internal capsule. I have never found any evidence of this, or any other anastomosis within the brain substance. Beevor and Aitken have both denied the existence of the lenticulo-optic artery of Duret and Charcot. In this enquiry no trace of this vessel could be found.

Summary

1. In apes and Man the cerebral arteries form the same closed network as in lower animals. The major channels picked out—the anterior, middle and posterior cerebral arteries—are the same.

2. The anterior cerebral artery follows the same course as in sub-Primates, but has taken over some of the field of the middle cerebral artery because of

the bending of the endorhinal fissure. Thus, in addition to its own field of supply, the anterior cerebral artery comes to supply some of the most anterior part of the hypopallial derivatives, the lateral part of the olfactory bulb and some of the orbital surface of the frontal lobe. The expansion of the general cortex has increased the area of neopallial distribution of this vessel.

3. The middle cerebral artery has surrendered some of its striatal and palaeo-olfactorial distribution to the anterior cerebral artery. Otherwise its field of supply has only altered in so far as the growing neopallium demanded.

4. The anterior choroidal artery has acquired additional hippocampal and choroidal branches. Otherwise its field of supply is little changed. This vessel supplies most of the globus pallidus, usually the corpus subthalamicum and ventro-lateral nucleus of the thalamus, and the upper parts of the substantia nigra and red nucleus as well as the ansa lenticularis. Kinnier Wilson (40) has shown that the globus pallidus is connected with these other cell masses through the ansa, and it would appear that this part of the anterior choroidal artery is the channel chosen to supply the components of this single functional unit (see fig. 10).

5. The posterior cerebral artery has consolidated its most posterior stem of origin in the anterior mid-brain channels, but variations are not infrequent. The cortical field of supply shows an increase to meet the greater neopallial demands. Its supply to the tail of the caudate nucleus may be taken over by the anterior choroidal artery as Beevor has shown.

6. The basal ganglia have developed upon the lines laid down in lower Mammals. The palaeo-striatum has formed the medial part of the amygdaloid nucleus and the tail of the caudate nucleus (primitive amygdala), the globus pallidus and infero-medial part of the head of the caudate-putamen mass. The hypopallium has developed into claustrum, putamen, supero-lateral part of the head of the caudate-putamen mass, the body of the caudate nucleus and the antero-lateral part of the amygdaloid nucleus. The blood supply remains constant.

7. The blood supply of the internal capsule is the same as in lower Mammals, but it should be noted that the internal capsule has increased greatly in size and has a definite infralenticular part which has nearly cut off the amygdaloid nucleus from the rest of the basal mass. This has caused a considerable attenuation of the tail of the caudate nucleus (fig. 11).

8. Whenever the terminal arterioles enter the brain to reach their final area of distribution they become end-arteries. There is no evidence that sub-cortical arterial anastomosis ever occurs.

GENERAL SUMMARY

1. In Fishes the fore-brain is composed mainly of palaeo-olfactorium and is enveloped within a closed network of arteries. In this network two channels—the medial and lateral olfactory arteries—have become enlarged

to carry the main stream of blood. These channels run close to the grooves separating the palaeo- and neo-olfactoria and share equally the blood supply of both. The palaeo-olfactorium receives the richer supply.

2. In the frog the arterial network remains intact. The vessels reflect the regressive state of the brain but show an advance upon the condition of the Fish. The common ancestor of frog and Reptile probably possessed separate anterior, middle and posterior cerebral arteries, but the frog has only medial and lateral olfactory arteries. The medial olfactory artery is the same as in the Fish, but the lateral, having shifted its origin posteriorly, arises from one of the diencephalic vessels. It has three main sets of branches: hippocampal, pyriform and striatal. The striatal branch is the representative of the lateral olfactory artery of the Fish while the hippocampal and pyriform branches have evolved from the arterial anastomosis over the neo-olfactorium.

3. Reptiles have formed separate anterior, middle and posterior cerebral arteries from the arterial network. The anterior cerebral artery has developed from the medial olfactory artery but its main stream of blood has been diverted to the medial wall of the hemisphere, especially to the paraterminal body. The middle cerebral artery represents the combined pyriform and striatal branches of the lateral olfactory artery of the frog, but it has a direct connection with the cranial division of the internal carotid artery which is diminutive in the frog. The posterior cerebral artery has arisen from the lateral olfactory artery and is devoted mainly to the hippocampal region.

4. In lower Mammals the cerebral arteries have to cope with the demands of the growing neopallium. The dorso-posterior expansion of the hemispheres has caused the posterior cerebral artery to employ successively posterior stems of origin until it receives its blood through anterior mid-brain channels. The basilar artery enlarges to carry the increased supply. The posterior cerebral artery still supplies most of the hippocampal formation and has enlarged to meet the demands of its share of the neopallium. The anterior choroidal artery has evolved from the inferior cerebral artery, cf. *Sphenodon* (and its representative in other Reptiles) by the acquisition of choroidal branches from the posterior cerebral artery. The middle cerebral artery sends most of its blood to the pyriform lobe and neopallium but its old course and distribution in the anterior endorhinal fissure are subserved by small branches running forwards to the olfactory bulb. The anterior cerebral artery again sends most of its blood to the medial hemisphere wall to supply the paraterminal body and commissures, and the supracallosal hippocampus, and especially the neopallium. The three cerebral arteries anastomose at the periphery of their fields of supply and maintain the primitive vascular network.

5. In Primates the cerebral arteries complete the developmental tendencies of the sub-Primates. The posterior cerebral artery is usually constant in its mid-brain origin. The anterior choroidal artery has acquired some further choroidal branches. The middle cerebral artery observes the same course and

relations as in lower Mammals but has surrendered some of its supply to the anterior cerebral artery. The anterior cerebral artery has only altered in its acquisition of some of the middle cerebral field of supply. The primitive network is intact.

6. The evidence of vascular distribution supports the view that the hypopallium of Reptiles has formed the claustrum, putamen, body of the caudate nucleus, supero-lateral part of the head of the caudate-putamen mass and the lateral part of the amygdaloid nucleus. The palaeo-striatum has given rise to the infero-medial part of the head of the caudate-putamen mass, the globus pallidus, the medial part of the amygdaloid nucleus and the tail of the caudate nucleus. The tail of the caudate nucleus appears to be the incompletely split-off part of the primitive amygdala. The vascular supply of the various parts of the basal ganglia is constant from Fish to Mammal.

7. Heubner's artery is the survivor of the anastomoses over and around the palaeo-olfactorium. As this primitive vascular ring becomes crowded together with the closing up of the endorhinal fissure most of the channels revert to their originally diminutive condition, but one remains large. This vessel obtains most of its blood from the anterior cerebral artery but retains its old connection with the middle cerebral artery. It supplies most of the palaeo-olfactorium and the infero-medial part of the head of the caudate-putamen mass and the anterior part of the globus pallidus; from the middle cerebral artery it takes over the supply of some of the most anterior part of the corpus striatum.

8. The internal capsule has a composite blood supply. The anterior cerebral artery supplies the inferior half of the anterior limb, and the anterior choroidal the posterior two-thirds of the posterior limb to the upper level of the globus pallidus. The middle cerebral artery supplies the upper parts of both limbs and the posterior communicating artery the region of the genu.

9. However much cerebral arteries anastomose over the surface of the brain, they become end-arteries whenever they enter the brain substance. There is no evidence that sub-cortical anastomoses ever occur.

10. Every cerebral artery has evolved from a primitive vascular network enveloping the brain. From this net channels have become enlarged in response to the demands of the parts they supply. The principles which govern the formation of cerebral arteries are:

(*a*) Functional constancy: whenever a neural mechanism evolves an artery develops for its supply and this neuro-vascular mechanism remains constant throughout evolution.

(*b*) Economy of distribution: when two or more end-arteries lie close together they employ a common vessel of distribution.

(*c*) Convenience of source: if a distributing channel becomes separated from its source it obtains blood from a nearer source by the enlargement of existing anastomotic channels.

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A NOTE ON THE PEDUNCLE OF THE FLOCCULUS AND THE POSTERIOR MEDULLARY VELUM

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Despite the vast amount of literature which has grown up in recent years concerning the cerebellum in general, and the flocculus in particular, the peduncle of the flocculus, as a macroscopical anatomical entity, has not attracted much attention. I was led to carry out a series of blunt dissections in this region of the brain in an endeavour to determine whether the posterior medullary velum is to be regarded as a single entity stretching across the median plane, as it is described and figured in most English and in many continental text-books of Human Anatomy, or as a bilateral structure as described in Testut's *Traité d'Anatomie Humaine* and elsewhere. The examination of the velum led me subsequently to explore the peduncle of the flocculus, and the description of the latter will be facilitated if the posterior medullary velum is first considered in detail.

THE POSTERIOR MEDULLARY VELUM

Before a satisfactory view of the posterior medullary velum can be obtained, the anterior part of the inferior aspect of the ansiform lobule (lobulus biventer) must be taken away by blunt dissection. In this way good access is obtained to the tonsil, which must be removed from the recess in which it lies. When this step is carried out carefully, the furrowed band (of Reil) is exposed in the postero-medial part of the recess passing from the lateral aspect of the uvula to the postero-medial aspect of the tonsil. The velum is now completely exposed in the floor of the recess from which the tonsil has been removed. It forms a thin, frequently translucent, sheet, continuous along its concave anterior margin with the epithelial part of the roof of the fourth ventricle, and more laterally with the epithelial floor of the lateral recess. When the epithelial roof of the ventricle is torn away, the anterior margin of the velum is converted into a free border (fig. 1) and can be traced laterally into the peduncle of the flocculus.

The lateral and posterior limits of the velum form a continuous curved border, along which it is connected to the white core of the cerebellar hemisphere. The medial border of the velum reaches and blends with the side of the nodule. The precise character of this relationship can be determined only after examination of the nodule and of microscopical sections (see later). When the nodule is poorly developed, the velum reaches the side of the anterior part of the uvula. The inferior surface of the velum is covered with pia mater and

is related to the blunt upper end of the tonsil. The superior surface of the velum is covered with ependyma and forms the lower wall of the slit-like "posterior superior ventricular recess," clearly shown in Retzius' figure of a cast of the ventricles of the brain, reproduced in most text-books of anatomy. The upper wall of this recess is formed by the white core of the cerebellum and contains the nuclei dentatus, emboliformis, globosus and fastigii.

It should be observed that, occasionally, the grey substance of the nodule is continued laterally along the anterior part of the inferior surface of the velum almost to the flocculus and that, more frequently, isolated patches of grey substance may be present in the same situation. This condition has also been noted by Papez (1).

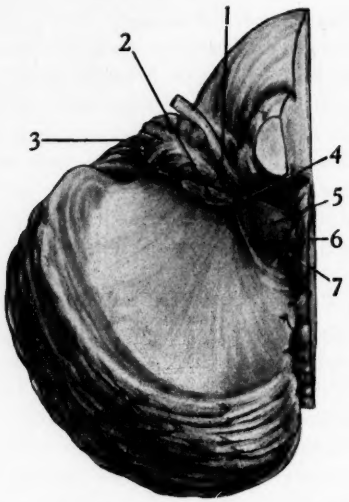

Fig. 1. Dissection to expose the right posterior medullary velum from below. 1, Acoustic nerve; 2, secondary flocculus; 3, flocculus; 4, peduncle of flocculus; 5, posterior medullary velum; 6, edge of tonsillar recess; 7, furrowed band (of Reil). N.B. The epithelial part of the roof of the fourth ventricle has been torn away.

The structure of the velum is admirably shown in Ziehen's (2) figures (305, 307, etc.). A single layer of ependymal cells clothes its upper surface and is succeeded by a layer of reticulated neuroglia. The next layer consists of medullated nerve fibres running in different directions, and it varies considerably in thickness in different brains. A second, thin, layer of neuroglia covers the inferior surface (fig. 2).

Before the precise character of the relationship of the velum to the nodule can be appreciated, the form and structure of the latter must be considered. The surfaces of the nodule may be designated "ventricular" and "uvular." The ventricular surface is usually somewhat curved in its long axis, being

convex forwards and upwards, although sometimes, when the nodule is poorly developed, the whole surface is directed upwards. Four, or five, folia separated by three, or four, short fissures cover the ventricular surface, but they are always restricted to its anterior (or peripheral) part. The posterior (or central) part of this surface is devoid of any covering of grey substance, and its white substance is exposed in the lower wall of the dorsal median recess of the roof of the ventricle. The number of folia and fissures on the uvular surface always exceeds the number on the ventricular surface, and there is always one and frequently there are two folia on this aspect which have no corresponding folia on the ventricular aspect (fig. 3). The fissures on both surfaces terminate blindly, when traced laterally, and the lateral portions of the folia become continuous with one another, on both aspects.

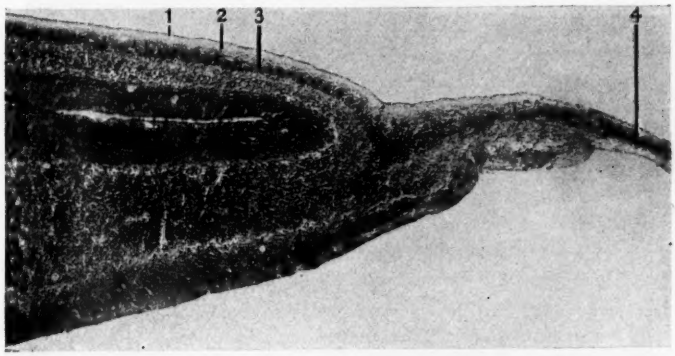

Fig. 2. Coronal section through the nodule and adjoining part of the posterior medullary velum. 1, ependyma on nodule; 2, subependymal neuroglia; 3, white substance of nodule; 4, medial part of posterior medullary velum.

The lateral aspect of the peripheral part of the nodule is covered with grey substance anteriorly and along its margins, but presents a narrow intermediate zone where its white core would be exposed, were it not directly continuous with the nervous layer of the posterior medullary velum. It is essential to observe the behaviour of the ependymal layer of the velum when it reaches the nodule. Posteriorly it passes without interruption on to the exposed white substance of the central end of the ventricular surface (fig. 2); anteriorly, it passes on to the epithelial roof of the ventricle and is separated from the grey substance of the ventricular surface of the nodule by a double layer of pia mater and fringes of choroid plexus (fig. 3).

A coronal section through the posterior (or central) part of the nodule and the adjoining part of the posterior medullary velum is shown in fig. 2. The ependymal layer and the subependymal neuroglia pass on to the exposed white substance of the nodule, but the white fibres intermingle with its white

core. An approximately median sagittal section through the nodule is shown in fig. 3. It will be seen that the grey substance of the ventricular surface is separated from the ependyma by a double layer of pia mater and fringes of chorioid plexus, whereas, dorsally, the ependyma lies in immediate contact with the white substance.

The history of the nomenclature of the velum is summed up by Burdach (3). It was first described by Tarin, who regarded it as a bilateral structure and named it "Valvulae semicirculares posteriores superiores." His description was accepted and followed by Malacarne and Vicq d'Azyr. Reil, however, regarded it as a single entity, but he included the whole of the nodule as its

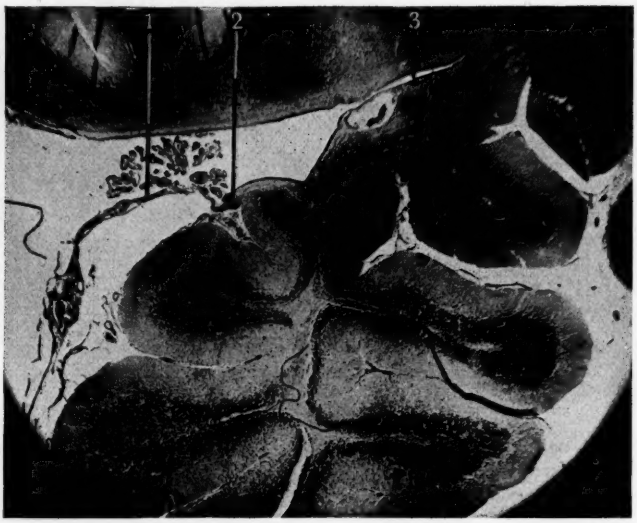

Fig. 3. Median sagittal section through nodule. 1, epithelial roof of fourth ventricle, from which, at 2, the ependyma passes dorsally on to the surface of the nodule; 3, dorsal median recess of roof of fourth ventricle.

median part and defined the complete formation as an inter-floccular commissure. Meckel, following Reil, introduced the term "posterior medullary velum." At the present time it has become customary to regard the ependyma in the central part of the ventricular surface of the nodule and its underlying neuroglia as the median part of the velum, which has become blended with the nodule, but this interpretation tends to give a very misleading impression.

Ingvar (4), as the result of a detailed study of the phylogeny of the cerebellum, has come to the conclusion that the posterior medullary velum represents all that remains of a cortical continuity between the nodule and the flocculus. This view appears to me to be incontestable and it receives additional

support, if that were needed, from the occasional extension of the grey substance of the nodule on to the inferior surface of the velum and the more frequent occurrence of isolated patches of grey substance in the same situation.

The posterior medullary velum represents an area in the posterior lobe of the cerebellum on each side where the grey substance has atrophied and disappeared, and it is therefore a bilateral structure. It does not, and cannot, exist in the median plane, where the posterior lobe is represented by the nodule, uvula and pyramid.

THE PEDUNCLE OF THE FLOCCULUS

The flocculus, though small, is a well-developed structure in the human brain, although the secondary flocculi, which presumably represent the paraflocculus, are poorly developed and variable in size and number. Owing to its phylogenetic history the flocculus has received much attention from neurologists and neuro-anatomists and its connections have been explored in many mammals with a view to obtaining some light on its functional activities. Most of the work in this connection has been done on rabbits, cats and dogs and very few references are to be found in the literature to the human brain, since Bruce (5) (and later Hoesel (6)) showed that the fibres of the floccular peduncle are the first of the cerebellar fibres to become myelinated. Bruce (5) demonstrated that the fibres of the peduncle are connected with the medial vestibular nucleus, and the ventral cochlear nucleus, and with the nucleus of the sixth cerebral nerve of the same side. In addition, he described a bundle of fibres which ascend in the floor of the fourth ventricle.

Ten years later Horsley and Clarke (7) traced efferent floccular fibres to the nucleus fastigii and emphasised the fact that, in the cat, these fibres avoid the dentate nucleus. Löwy (8) (1911) extirpated the flocculus in rabbits and, using the Marchi method, traced fibres to the superior vestibular nucleus (Bechterew), the sixth nucleus of the same side—thus confirming Bruce's observation in the human foetus—and, by way of the superior cerebellar peduncle, to the nuclei of the trochlear and oculomotor nerves of the opposite side.

These connections with the nuclei of the third, fourth and sixth cerebral nerves received additional support from the experimental work of Bárány (9). Using double electrodes he stimulated the cortex of the flocculus in rabbits and obtained eye movements of a nystagmic character. Subsequently, the portions stimulated were excised and nystagmic movements of the eyes in the opposite direction resulted.

The whole literature on the subject has been reviewed by Kappers (10), and still more recently by Ziehen (2). Kappers rejects Bolk's (11) view that the flocculus is concerned with the movements of the tail, and, accepting the conclusions of Bruce, Löwy, Bárány and others, definitely associates the flocculus with the control and regulation of the tonus of the eye muscles.

Ziehen is non-committal with regard to the functional aspect of the question, but he does not accept as proven any connections between the flocculus and the motor nuclei of the third, fourth and sixth nerves. He regards as definitely established: (1) connections with other parts of the palaeo-cerebellum; (2) both flocculo-fastigial and flocculo-dentate fibres; (3) vestibulo-floccular fibres; and (4) an efferent bundle from the flocculus to the region of the locus coernuleus and the mid-brain.

DISSECTION OF THE PEDUNCLE OF THE FLOCCULUS

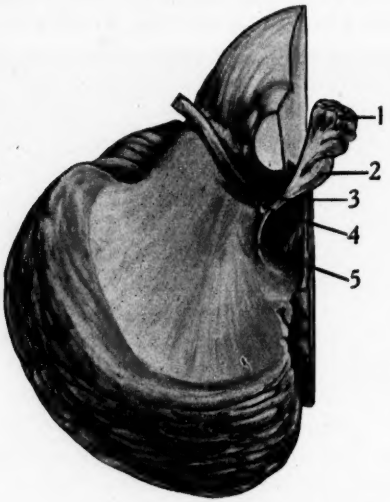

Fig. 4. Dissection of the peduncle of the flocculus. 1, flocculus, turned downwards and medially; 2, secondary flocculus; 3, Peduncle of flocculus; 4, ventral fibres passing to floor of fourth ventricle; 5, dorsal fibres passing to furrowed band.

On attempting to obtain a view of the isolated peduncle of the flocculus in the human brain, I was surprised to find how easily and simply it could be dissected, at least in the neighbourhood of the lateral recess of the fourth ventricle. After the exposure of the posterior medullary velum and the removal of the epithelial roof of the fourth ventricle, the pia mater must be removed carefully from the apex of the flocculus and the adjoining part of the brachium pontis. A thin layer of surface neuroglia connects the deep or upper surface of the flocculus to the brachium pontis. When this has been torn through, the flocculus can be turned downwards and medially and its peduncle can be elevated from the brachium pontis and the restiform body (fig. 4). The separation of the secondary flocculi can be effected at the same time, but the process is not so satisfactory, as it is impossible to be certain that no fibres of the brachium pontis have been taken with it. The peduncle

of the flocculus can be traced without difficulty to the lateral angle of the fourth ventricle, where it expands into a somewhat triangular central sheet, with very much thickened ventral and dorsal borders.

The fibres on the ventral border form a substantial fasciculus, which is closely related at first to the acoustic nerve (fig. 4). It separates from the other fibres and turns upwards and medially in the lateral part of the fourth ventricle. It constitutes the pedunculus flocculi of Burdach (3), and will be referred to in greater detail when the rest of the peduncle has been considered.

The fibres in the dorsal border of the sheet can be followed backwards and medially round the margin of the tonsillar recess and most, if not all, can be traced into the furrowed band. These fibres seem to comprise the whole of the peduncle of the secondary flocculi and a few fibres from the flocculus itself. The thin, triangular sheet of fibres soon loses continuity with the thick ventral bundle and passes upwards and medially in the lateral wall of the tonsillar recess. It reaches the lateral limit of the posterior superior ventricular recess and there splits into two fine layers, of which the lower passes into the posterior medullary velum and the upper into the upper wall of the ventricular recess. These three groups of fibres represent the connections with other parts of the palaeo-cerebellum and the flocculo-fastigial and flocculo-dentate pathways.

The ventral bundle, however, carries off the majority of the fibres of the floccular peduncle and it can be traced considerably further by blunt dissection. It passes upwards and medially close to the lateral limit of the floor of the fourth ventricle. Very soon, it gives off a number of fine sheets of fibres which run medially and slightly downwards. They can only be followed for a short distance as they tend to sink more deeply into the substance of the pons. In some cases a single bundle of these fibres courses immediately under the ependyma and is visible to the naked eye, constituting one of the striae medullares (fig. 5). When present, it can be followed to the median plane. These fibres represent vestibulo-floccular and flocculo-vestibular connections and, in addition, presumably, the flocculo-abducent fibres, described by Bruce and Löwy.

After these connections have been given off, the ventral bundle, much reduced in size, continues upwards and medially. In most cases one can demonstrate that a slender fasciculus leaves its lateral side and ascends in the brachium conjunctivum, but its subsequent destination is impossible to determine by blunt dissection. Occasionally, too, one can display a similar fasciculus leaving its medial side and with a more medial inclination. It can be traced almost to the upper limit of the ventricular floor, and is then close to the median plane. The remainder of the ventral bundle (Obersteiner's (12) "Fasciculus lateralis fossae rhomboidalis") continues its upward and medial direction, along the lateral limit of the upper part of the floor of the fourth ventricle and crosses the dorsal aspect of the locus coeruleus (fig. 5). The fasciculus stands out clearly against the blue background and some of the

fibres may terminate in its substance. The great majority of the fibres, however, can be traced further and are found to pass under cover of the lateral part of the inferior colliculus and the adjoining terminal part of the lateral lemniscus, where they turn forwards. As they do so, they commence to diverge and I found it impossible to follow them further.

These ascending fibres from the peduncle of the flocculus were first observed by Burdach (3), who described them as ascending along the floor of the cerebral aqueduct to the floor of the third ventricle. They constitute the pedunculus flocculi sagittalis of Ziehen (2). Owing to the methods employed

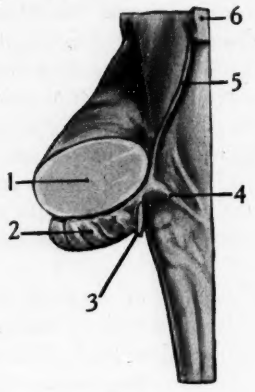

Fig. 5.

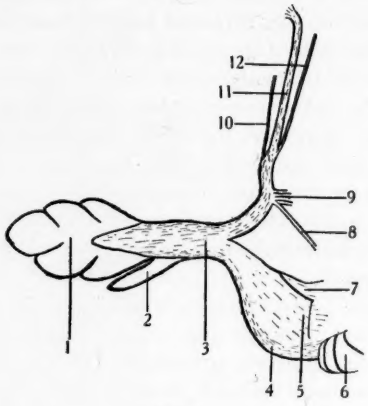

Fig. 6.

Fig. 5. Dissection of the ascending ventral fibres of the peduncle of the flocculus. 1, brachium pontis (cut); 2, flocculus; 3, dorsal fibres of floccular peduncle (cut); 4, fasciculus from ventral part of floccular peduncle, visible in floor of fourth ventricle; 5, ascending fibres from ventral part of floccular peduncle, crossing locus coeruleus; 6, inferior colliculus.

Fig. 6. Diagram of the peduncle of the flocculus and its offsets, as determined by blunt dissection. 1, flocculus; 2, secondary flocculus; 3, peduncle; 4, fibres passing to furrowed band; 5, posterior medullary velum (with cut edge, medially); 6, furrowed band; 7, fibres in upper wall of posterior superior ventricular recess; 8, bundle visible in floor of fourth ventricle; 9, connections with vestibular and abducent nuclei; 10, slip to brachium conjunctivum; 11, bundle ascending across the locus coeruleus; 12, slip found in some specimens.

in this investigation, it is, of course, impossible to do more than hazard a speculative suggestion as to the destination of the fasciculus. In the light of the work of Löwy (8) and Bárány (9), they might reasonably be regarded as an efferent pathway to the nuclei of the third and fourth cerebral nerves, and it is not beyond the bounds of possibility that some may join the medial longitudinal bundle and others may be destined for the red nucleus.

I am much indebted to Dr E. B. Jamieson, who was responsible for the query concerning the precise character of the posterior medullary velum, for

it has led me to gain a much clearer conception both of the velum and of the floccular peduncle. I am indebted also to Mr J. E. Clapton, for the drawings which are reproduced as figs. 1, 4 and 5.

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THE GROSS ANATOMY OF THE LATERAL VENTRICLES

By A. TORKILDSEN, M.D.[1]

INTRODUCTION

Previous papers on the gross anatomy of the cerebral ventricles have been based upon casts and dissection of human brains (Key and Retzius, 1875; Welcker, 1915; Locke and Naffziger, 1924; Locke, 1925). They have been, consequently, subject to several important sources of error such as alteration caused by the fixation of the brain and an injection pressure great enough to cause dilatation of the cavities. Some workers have not obtained a successful cast until they met with a brain with dilated ventricles, and the depicted cast thus presents a moderate but definite case of hydrocephalus.

The author has employed another technique, realising that the anatomy of the ventricles in a living brain is somewhat different from that seen at dissection or as a result of injection. For this purpose casts and dissection of the brain have been correlated with the roentgenological pictures of the ventricles after the cerebrospinal fluid has been exchanged for air. Intraventricular air accidentally introduced had been demonstrated on the X-ray film (Luckett, 1913; Skinner, 1916) before Dandy (1918) introduced ventriculography as a diagnostic method, but it is only since this method has become commonly used that examination of innumerable ventriculograms has given us a detailed knowledge with regard to the cerebral ventricles.

Several variations from the usual anatomical conception have been found and will be described in detail. This is especially true of the posterior part of the lateral ventricle and of the posterior horn in particular.

It has been often questioned whether the foramina of Luschka and Magendie are normal openings present in life or artefacts caused by the manipulations of the brain after death. The introduction of air into the ventricles after it has been injected by lumbar puncture into the spinal canal proves, however, that at least one of these openings must be physiologically present.

TECHNIQUE

Material

For the present purpose eleven brains from adults have been used. The youngest patient was 18 years of age and the oldest 68. All of these patients had died of diseases not connected with the central nervous system, and the brains were fixed in formalin.

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A group of 450 selected sets of ventriculograms and encephalograms has been studied and from this thirteen sets were chosen for the present purpose because they illustrate particularly what we consider, in our experience, to be a normal ventricular system.

Most of these cases were epileptic patients; some of them were cases of post-traumatic headache and some of them suffered from headache of unknown origin. Neoplasms have not been verified in any of the cases. The youngest was 17 and the oldest 48 years of age.

Methods

Two different methods have been employed:

A. One method for the study of the brains and making casts of these.

B. One method for the study of the ventriculograms.

Both methods have been used to decide the same distances and sizes.

Method A

The procedure has been to insert one "brain needle" in the anterior horn, one in the posterior and one in the inferior horn. The needles were of the type commonly used for brain puncture.

The one in the anterior horn was used for injection of melted paraffin (melting point 56° C.), the other two were used as outlets in order to allow the cerebrospinal fluid and air to escape.

The paraffin was injected under pressure of about 1000 mm. of water in order to expel the fluid which was already in the ventricles and in order to hasten the procedure so that the paraffin should not solidify before the entire space had been filled with the substance. This pressure, however, was not great enough to alter the form of the ventricular cavity. Further, the pressure offset the tendency for the paraffin to shrink when solidified.

In order to delay the solidification until the entire space had been filled with paraffin, the rubber tube through which the fluid was running was irrigated constantly with warm water at a temperature between 70 and 80° C., and the brain had been kept in water at 35° C. for 2 hours prior to injection.

When the injection of paraffin had been continued long enough to secure complete expulsion of fluid and air, the surface of the brain and the needles through which the paraffin escaped were irrigated with cold water, causing solidification of the paraffin and preventing further escape of the injected substance. In the meantime the fluid paraffin was kept under the same pressure as before in the needle for injection in order to obtain the best possible filling of the lumina. When the injected mass had solidified in the needle also, the procedure was interrupted and dissection of the brain was undertaken.

During the dissection the distance from the surface of the brain to the ventricle was measured at several points (fig. 10), and the dissection was done in such a manner that the thalamus was left intact in order to give support to the ventricle which was uncovered finally and could be measured.

Findings.

Fig. 1 outlines those parts of the ventricle which have been measured.

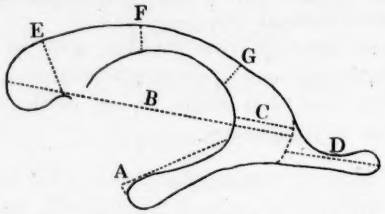


Fig. 1. Sketch showing those distances and portions of the lateral ventricle which have been measured.

As the posterior horn is not a constant part of the ventricles, the distance indicated by ***B*** in fig. 1 was measured in each case whether or not a posterior horn was present. ***B*** represents the distance from the anterior horn to the furthermost part of the ventricle regardless of the posterior horn. This manner of measuring the total length of the lateral ventricles is not quite exact, but it is the only way by which comparison can be made.

The following measurements were found:

Left ventricle

(All measurements shown are centimetres.)

	A	*B*	*C*	*D*	*E*	*F*	*G*
Brain 1	3·0	7·5	2·0	1·2	2·0	0·5	0·7
Brain 2	5·0	7·9	2·1	0·8	2·1	1·0	0·8
Brain 3	3·8	7·5	1·9	0·0	1·9	1·0	0·9
Brain 4	4·0	7·9	2·1	0·3	1·6	0·6	0·8
Brain 5	5·0	8·0	1·8	2·0	1·6	0·6	0·6
Brain 6	3·9	8·0	2·0	3·4	1·9	0·5	0·5
Brain 7	4·0	8·1	2·1	0·0	1·7	0·6	0·7
Brain 8	4·0	7·9	1·9	3·6	2·1	0·5	0·5
Brain 9	4·2	7·8	2·0	0·7	1·8	0·7	0·5
Brain 10	4·0	7·9	1·8	0·3	2·0	0·5	0·7
Brain 11	4·0	8·0	2·0	3·0	2·0	0·6	0·7
Average	4·08	7·85	1·97	1·39	1·88	0·64	0·69

Right ventricle

	A	*B*	*C*	*D*	*E*	*F*	*G*
Brain 1	2·5	7·5	1·5	1·3	1·8	0·5	0·7
Brain 2	4·8	8·0	2·0	0·8	2·1	1·0	0·9
Brain 3	3·0	8·0	2·0	0·0	2·0	1·2	1·0
Brain 4	4·3	8·0	1·9	0·4	1·7	0·6	0·8
Brain 5	5·0	7·9	1·8	2·0	1·5	0·5	0·6
Brain 6	3·8	7·9	2·1	3·3	1·9	0·5	0·6
Brain 7	4·1	8·1	2·1	0·0	1·7	0·6	0·6
Brain 8	4·2	7·8	1·9	3·6	2·1	0·5	0·6
Brain 9	4·1	7·8	2·1	0·8	1·8	0·7	0·5
Brain 10	3·9	8·0	1·9	0·4	2·0	0·6	0·6
Brain 11	4·0	8·0	1·8	3·4	1·8	0·6	0·6
Average	3·97	7·90	1·91	1·45	1·94	0·66	0·67

These measurements employed give the results shown in fig. 2.

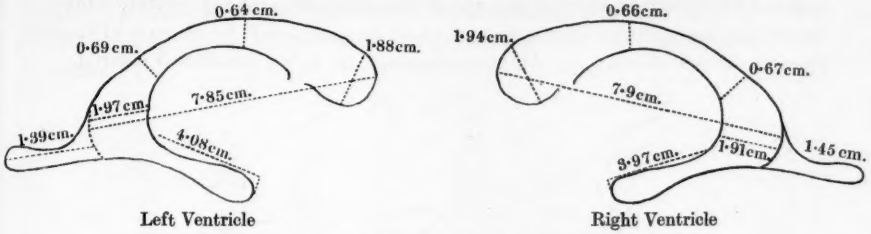


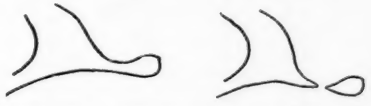
Fig. 2. Sketch showing the findings of the left and right ventricle.

Discussion of the findings. By looking at the two tables one will see that the two parts of the lateral ventricle which show the greatest variation are the posterior and inferior horns.

As already mentioned the posterior horn is not constantly present. In two of the eleven cases the posterior horn was entirely absent. On the other hand, a posterior horn as long as 3·6 cm. was found and in both cases the ventricles had to be considered normal.

It is important to note that in some cases where the calcarine fissure was a rather deep one it seemed to cut in far enough to obliterate the posterior horn.

In other cases there was constriction of the middle part of the posterior horn so that the posterior portion was considerably wider than the middle portion (see fig. 3), and in one of these cases the horn was completely constricted with a cavity posterior to the obstruction (fig. 4).



Figs. 3 and 4. Variations of the posterior horn.

That part of the ventricle other than the posterior horn which showed the greatest variation was the inferior horn. The shortest inferior horn that was found measured 2·5 cm. and the longest 5 cm.

Because it is difficult to determine the border between the posterior horn, the inferior horn and the body of the ventricle, these findings are of approximate value only.

The anterior horn varied in height from 1·6 to 2·1 cm., and the middle and posterior part of the body varied from 0·5 to 1·2 cm. and 0·5 to 1 cm. respectively.

The posterior portion of the body of the lateral ventricle was found to have a rather variable shape (see fig. 5 A, B and C). The difference in appearance of this portion of the ventricle depends upon the splenium of the corpus callosum

which forms the posterior wall at this point. As the illustrations show, the body of the ventricle may at this point run smoothly into the posterior horn, but it may also occur with the formation of an angle, and the incisura at times shows a double formation. All three features are to be considered normal.

Fig. 5. Variations of the posterior portion of the lateral ventricle.

The length of the lateral ventricle was fairly consistent with a variation from 7·5 to 8·1 cm.

Thus it can be seen that the size of the normal lateral ventricle is not constant as it shows considerable variation, especially of the inferior and posterior horns.

Method for making a lead cast from the paraffin cast.

After the paraffin cast had been dissected free from the brain it was put in plaster of Paris, having been furnished with four columns of paraffin which should serve as vents for the escape of air while the casting is being done. Fig. 6 shows the position of the vents.

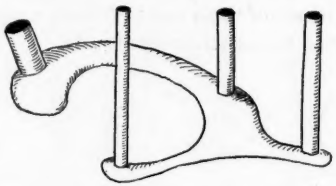


Fig. 6. The ventricular cast furnished with vents ready for casting in plaster of Paris.

The ventricular cast with the columns was then placed in plaster of Paris and after this had solidified it was heated sufficiently to melt away the paraffin. Then the empty cavity was filled with lead, the plaster broken away and finally the lead columns in the vents were removed.

In order to obtain a brass model the lead ventricles can be cast in sand.

Method B

Study of ventriculograms and encephalograms.

When an encephalogram or ventriculogram has been successfully performed one can measure the picture of the ventricle on the X-ray film and, by taking into consideration the extent of the magnification, one can find the

actual size of the ventricle. This can be done by mathematical methods. The following tables show the results of thirteen examinations, and from fig. 7 one can see which distances have been measured. The sizes are indicated in centimetres.

Left ventricle

	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*
	4·0	1·0	0·5	7·9	1·0	1·4	1·8	1·5	1·1
	3·6	0·6	1·0	8·5	1·5	1·3	1·4	1·3	1·3
	3·5	0·5	0·5	8·5	2·0	0·0	1·0	1·5	1·3
	3·0	0·8	0·6	8·5	1·1	1·0	1·6	1·5	1·0
	4·2	0·4	1·1	8·5	1·5	0·0	1·0	1·2	1·3
	5·0	0·7	0·8	8·6	1·0	0·0	1·5	0·8	1·0
	3·5	0·5	0·5	8·6	1·3	1·5	1·5	1·3	1·1
	3·9	1·0	0·8	8·1	1·2	2·0	1·4	1·0	0·8
	3·0	0·7	0·7	8·5	1·5	3·0	2·0	1·6	1·0
	2·5	0·8	0·9	9·5	1·3	0·8	2·0	1·3	0·9
	3·2	0·7	0·7	9·0	1·7	0·0	1·5	1·5	0·8
	4·0	0·4	1·0	10·0	2·0	0·0	2·0	1·5	1·0
	3·5	0·5	1·0	9·0	1·6	2·0	1·5	1·0	0·8
	46·6	8·6	10·1	113·2	18·7	13·0	20·0	17·0	13·4
Average*	3·6	0·7	0·8	8·7	1·4	1·0	1·5	1·3	1·0
Average†	3·28	0·64	0·72	7·76	1·28	0·90	1·36	1·18	0·90

Right ventricle

	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*
	3·5	1·0	0·7	8·0	1·1	1·0	1·0	1·4	1·0
	2·5	0·5	0·5	8·2	1·1	1·3	1·8	1·1	1·1
	4·0	0·5	0·5	10·5	1·5	1·5	1·9	1·0	1·0
	3·3	0·5	0·4	8·0	1·5	2·0	1·7	1·6	1·0
	4·6	1·0	0·6	9·0	1·5	2·5	1·6	1·4	1·5
	5·0	0·7	0·6	8·8	1·4	0·0	1·5	0·8	1·0
	4·4	0·4	0·4	9·0	1·3	1·0	1·5	1·0	1·1
	5·6	1·0	0·6	8·7	1·2	2·0	1·2	0·7	0·9
	2·5	0·7	0·7	8·5	1·5	2·0	1·3	1·3	1·0
	2·6	0·7	0·7	9·0	1·5	1·3	2·0	1·0	1·0
	3·2	0·7	0·7	9·5	2·0	0·0	1·5	1·3	1·3
	4·0	0·5	0·5	10·0	2·0	0·0	1·7	1·5	1·0
	3·5	0·5	1·0	9·7	1·5	2·5	1·5	1·0	1·0
	48·7	8·7	7·9	116·9	18·7	17·1	20·1	15·1	13·9
Average*	3·7	0·7	0·6	8·9	1·5	1·3	1·5	1·2	1·1
Average†	3·38	0·64	0·55	8·1	1·28	1·18	1·36	1·09	1·0

* Average of above nos.

† Average of above nos. taking magnification into consideration.

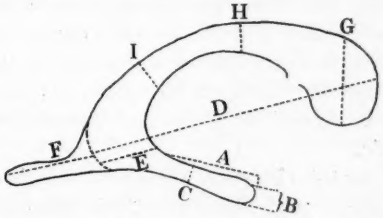


Fig. 7. Sketch showing the distances and portions of the lateral ventricles which have been measured on the X-ray film.

Discussion of the findings. The study of the ventriculograms showed, as has been pointed out previously, that the form and size of the lateral ventricles even under normal circumstances are not constant.

Examination of ventriculograms and encephalograms has taught us that considerable experience is necessary to pass judgment on variations from the normal ventricular form.

First of all it should be remembered that a gradual enlargement of the ventricles takes place during life because of general cerebral atrophy. In other words, if a person 15 years of age presents cerebral ventricles of the size which is normal at the age of 60, these ventricles should be considered abnormally large.

Then it is also our experience that the size and shape of the ventricles normally vary within certain limits in different individuals of the same age. This observation corresponds well with the findings by making casts of the ventricles and with the results of dissection. A ventricular shadow on the X-ray plate is anatomically reliable only when the portion of the ventricle in

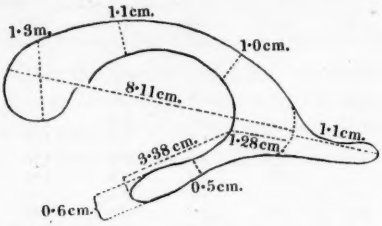


Fig. 8. Illustration of the findings concerning the right lateral ventricle.

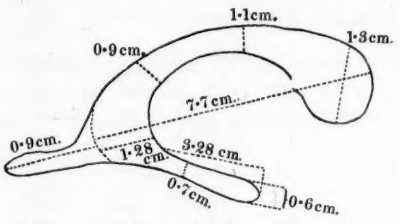


Fig. 9. Illustration of the findings concerning the left lateral ventricle.

question is completely filled. Some parts of the ventricles are difficult to fill well, and one should not attach, consequently, too much importance to the findings concerning such portions. This is especially true of the inferior horns.

The ventriculograms in the present series showed that the posterior horns are rather variable. All transitions were found, from complete absence to a length of 3 cm. The left posterior horn was absent in five out of thirteen cases, the right in three cases. The X-ray pictures which were used for the study of the posterior horns were taken with the occipital region as the highest portion. Consequently all the intraventricular air will ascend to that posterior portion and outline this completely on the X-ray plate, and an asymmetry in the X-ray picture must be caused by anatomical circumstances and not by defective filling with air.

The difference in the total length of the lateral ventricle varied from 7·11 to 9·5 cm. (regardless of the posterior horn). This difference is hardly greater than one would expect as a normal variation in normal individuals. The posterior portion of the body (*E* on fig. 7) was found to be from 1 to 2 cm. and

also on the ventriculograms the outline of this portion varied as seen in fig. 5. The individual variations of the height of the anterior horn were from 1 to 2 cm., but the outline and shape of this portion were more or less constant.

The average measurements, shown on p. 482, which were found by casts and by dissection, are not quite the same as those shown on p. 485, as a result of the study of ventriculograms.

The inferior horn appears shorter in the ventriculogram, probably because of incomplete filling with air.

The height of the anterior horn on the pneumograms is less than the height found by casting and by dissection, probably because the lowest portion of the anterior horn is narrow and not always well filled with air. In some cases it has been found to be less than 1 cm., while measurements taken by casting and by dissection never showed a lower measurement than 1·6 cm. On the other hand, in ventriculograms, measurements as high as 2 cm. were found which is only 1 mm. less than the highest of those found by the other method. One must, therefore, consider these measurements to correspond quite well.

The distance between roof and floor of the body of the ventricle also shows some variation. The greatest measurement found on the X-ray film was 1·5 cm. for the anterior portion of the body and 1·4 cm. for the posterior portion of the body. The reciprocal measurements found by the other methods were 1·2 and 1 cm. respectively. The lowest measurements were 0·75 cm. for the distance between roof and floor of the body of the ventricle on the pneumogram and 0·5 cm. for the same portion of the ventricle found by dissection and by casting.

The explanation of this difference must be the unavoidable collapse and shrinkage during the fixation. The collapse is obviously of greater importance than the shrinkage, because the total length of the lateral ventricle is very much the same by each method. The average length of the right and left ventricle, decided by study of X-ray plates, was 7·9 cm., and by casting and by dissection 7·87 cm.

The most posterior portion of the ventricle, where the posterior and inferior horns join the body, showed an average measurement of 1·94 cm. The average measurement of the same portion for right and left ventricles, decided by study of X-ray films, was 1·28 cm. The difference is again most likely due to incomplete filling with air. The highest measurement found by X-rays for this portion was 1·8 cm. and by casts 2·1 cm. The lowest measurements were 0·9 and 1·5 cm. respectively. This series is far too small to show how frequently the posterior horns are absent. It shows, however, that asymmetry of the posterior horns is frequently present and that at times one posterior horn is absent while the other is well developed.

The average length of the posterior horn was 1·75 cm. measured by casts and 1·5 cm. measured by X-ray films. The greatest measurement found by the casts was 3·6 cm. and by X-rays 2·7 cm.

The lateral ventricles in relation to the surface of the brain.

The distances from various points of the lateral ventricle to the surface of the brain have been measured. Figs. 10 and 11 show how this has been done. All the distances in fig. 10, except those concerning the inferior horn, have been measured from the surface of the brain at a point 2 cm. from the mid-line.

The two tables on p. 489 show the numbers which were found, and in figs 10 and 11 one can see these findings employed.

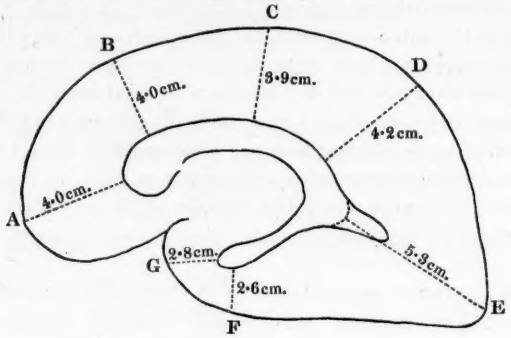


Fig. 10.

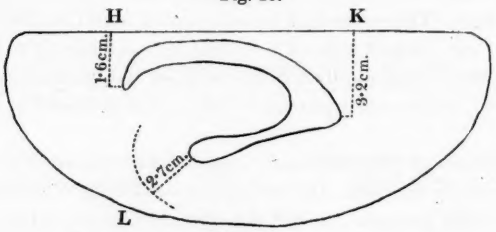


Fig. 11.

Figs. 10 and 11. Illustration of the distance from the lateral ventricle to the surface of the brain which has been decided by the study of X-ray films.

As the findings concerning the distance from the ventricle to the surface of the brain were about the same on the right and left (it does not vary more than 1 mm. anywhere), the measurements for the right side have been used in figs. 10 and 11 and no separate illustration of the left side has been made, as a difference of 1 mm. must be considered to be of little or no practical importance.

Discussion of the findings. The most striking feature in looking at fig. 10 is that the roof of the lateral ventricle follows the outline of the surface of the brain. The lateral ventricle is situated, however, so that the distance from the occipital pole to the posterior portion of the body is 1·3 cm. longer than from the anterior horn to the frontal pole. This figure shows that it is only in the posterior part that there is no "parallelism" between the ventricle and the surface of the brain, and even here the variation is only a slight one.

Such "parallelism" is also true regarding the inferior horn. Figs. 10 and 11 show that the distance from any part of the surface of the temporal pole to the inferior horn is more or less the same (2·6 cm., 2·7 and 2·8).

These figures show, however, that there is also a certain amount of variation of the distances in different individuals. The distance from the anterior horn to the frontal pole may vary as much as 1·3 cm., and the distance from the occipital pole to the posterior portion of the body may vary even 1·8 cm. A similar variation is true of all the other distances, all depending upon whether one is dealing with a large or a small ventricle.

Left ventricle

(All measurements in centimetres.)

	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*K*	*L*
Brain 1	3·5	3·8	4·0	4·0	5·5	3·5	3·5	2·0	3·0	3·5
Brain 2	3·3	3·4		(Compressed)			2·5	1·5	4·0	2·5
Brain 3	4·0	3·5	3·7	4·0	5·5	2·5	2·7	1·3	3·0	2·5
Brain 4	4·0	4·2	4·5	4·3	5·0	2·5	2·7	1·0	2·3	2·5
Brain 5	4·0	3·8	3·5	3·5	5·2	3·0	3·1	2·0	3·8	3·4
Brain 6	4·3	4·0	4·0	3·9	6·0	3·2	3·3	1·6	2·6	3·4
Brain 7	3·2	3·4	3·5	4·0	4·7	2·3	2·6	1·2	2·2	2·7
Brain 8	4·8	5·2	4·2	4·5	6·0	3·2	3·3	1·5	3·0	3·1
Brain 9	4·0	3·9	4·5	5·5	5·5	2·0	3·5	1·8	3·0	3·0
Brain 10	4·0	4·0	4·5	4·5	5·5	2·0	2·3	1·5	3·0	2·5
Average	3·9	3·9	4·0	4·2	5·4	2·6	2·9	1·5	3·2	2·7

Right ventricle

	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*K*	*L*
Brain 1	3·5	4·5	4·5	4·5	5·5	3·4	3·5	2·0	3·0	3·0
Brain 2	3·5	3·5	3·5	3·9	5·0	2·5	2·6	1·5	4·0	2·5
Brain 3	4·5	3·5	3·7	4·0	4·2	2·5	2·6	1·3	3·5	2·5
Brain 4	4·5	4·2	4·5	4·5	5·5	2·8	2·7	1·0	2·5	2·5
Brain 5	3·5	3·5	3·5	3·6	6·3	3·3	3·2	2·0	4·0	3·2
Brain 6	4·2	4·0	4·0	4·0	5·8	3·0	3·2	1·8	2·6	3·0
Brain 7	3·5	3·5	3·0	4·0	5·0	2·4	2·5	1·5	2·9	2·4
Brain 8	4·8	5·0	4·0	4·7	6·0	3·1	3·2	1·5	3·5	3·5
Brain 9	4·0	4·0	4·0	4·5	5·3	1·6	3·0	2·0	3·0	2·5
Brain 10	4·0	4·5	4·3	4·5	5·5	2·0	2·0	1·6	3·0	2·0
Average	4·0	4·0	3·9	4·2	5·3	2·6	2·8	1·6	3·2	2·7

The third and fourth ventricles.

In normal cases the third ventricle presents itself as a mere slit, a few millimetres wide. The majority of anatomical text-books describe the height and length as about equal, 2·5 cm. (Poirier and Charpy, 1921). The study of the third ventricle on the ventriculograms shows that in living humans the antero-posterior axis is somewhat longer than the height, and this form has, therefore, been given the third ventricle on the present model.

The aqueduct of Sylvius is approximately 2 cm. long and runs in an almost vertical direction. In order to strengthen the model it has been given a calibre greater than normal. The above mentioned authors give the length of the fourth ventricle as 3 cm. and the width as about 2 cm. The present model has been made according to this description as it corresponds well with the findings on the ventriculograms.

Description of the model. Because of its neurosurgical purposes, especially in connection with brain puncture and interpretation of ventriculograms, the greatest attention has been paid to the lateral ventricles. The lateral ventricles of the model are the actual casts of brain No. 11 on p. 482. It thus represents the normal ventricle, but according to the X-ray findings it is, perhaps, on the small side but well within normal limits.

On the left lateral ventricle the impression made by the thalamus, the caudate nucleus, the fornix and the splenium corporis callosi have been given separate colours in order to make it easier to visualise the relationship to the

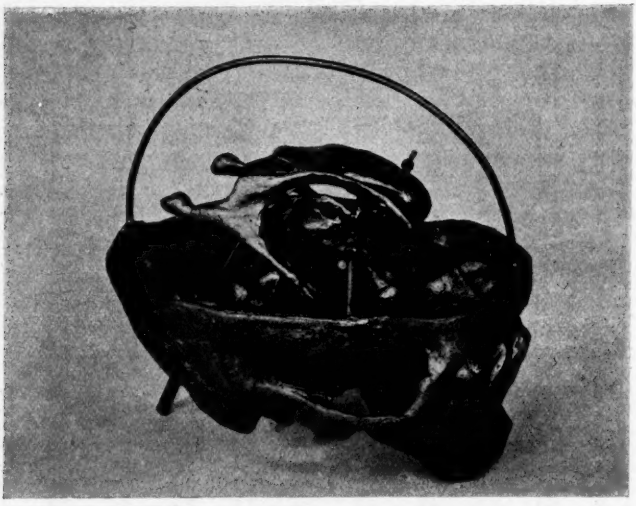


Fig. 12. Illustration of the ventricular model.

neighbouring structures. The lateral ventricle has been divided by black lines into six portions corresponding to units which can be recognised in the antero-posterior view of the ventriculogram. The four ventricles have been carefully placed in their normal positions with relation to each other.

The ventricular system has been placed in a partial cast of a skull of normal size on which a curved wire has been fixed, running from the front to the occiput, indicating the inner surface of the skull.

The ventricles can be moved from side to side in order to make it possible to demonstrate displacement of the ventricles quite clearly.

All pieces have been cast in brass. The model is on sale by the Pilling Surgical Instrument Company, Philadelphia, Pennsylvania.

SUMMARY

The size and form of the lateral ventricles have been decided by eleven paraffin casts and the study of 450 selected sets of ventriculograms.

The results of the examination by the two methods correspond very well but show that a certain amount of collapse takes place in the preparation of the brains.

The lateral ventricles vary to a certain extent in size and form. The greatest variation has been found in the posterior horns where the calcarine fissure at times seems to cause obliteration. The posterior horns are not constantly present, and a unilateral absence of a posterior horn can be seen in normal cases. The rest of the lateral ventricle is constantly present but varies within certain limits in size according to the size of the skull and age of the patient. Concerning the form of the lateral ventricles it has been found that there are normally certain variations of the posterior part of the body.

The investigations show that certain of the pictures and casts which previously have been supposed to represent the normal ventricles illustrate a moderate degree of hydrocephalus.

One of the paraffin casts which was considered to give a good picture of the normal ventricles has been reproduced in brass.

The casts which were obtained from the third and fourth ventricles have not been used for the present model. These parts have been artificially constructed according to anatomical description and ventriculographic findings. The distance from various points of the lateral ventricles to the nearest point at the inner surface of the skull has been measured. A normal skull has been cast in brass, the ventricular system has been placed in the skull and given the normal anatomical relationships.

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SOME OBSERVATIONS ON THE DEVELOPMENT OF THE CORPUS STRIATUM OF BIRDS, WITH SPECIAL REFERENCE TO CERTAIN STAGES IN THE COMMON SPARROW (*PASSER DOMESTICUS*)

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Studies of the avian hemisphere are sufficiently numerous to permit of a generalised conception of its structure in different forms. A small range of variation occurs in certain structural features, but the typically distinctive features are constantly encountered, particularly a marked reduction in the so-called cortical fields and a remarkable overgrowth of the corpus striatum. There is another feature of the avian hemisphere which is not devoid of significance, and that is the great preponderance of cells in the hemisphere as compared with the condition found in the Reptile. In the latter the cortical sheets which are relatively extensive are spread over the dorsal aspect of the hemisphere in a thin layer, and in the striatum itself cellular aggregation is not dense. The avian hemisphere on the contrary shows almost everywhere the same uniform field of densely packed cells separated into individual nuclear masses only by the thinnest laminae of fibres. Differentiation of the cortex from the subjacent grey matter, so obvious in many forms due to the lamination of cells in the former and their wide separation from other cell groups, can be seen only in certain localised regions in the avian hemisphere.

That the avian cortex may be only apparently reduced is a viewpoint which has been favoured previously. Elliot Smith (1919, 1919 *a*) has emphasised the fact that much of what is apparently striatal is in reality of cortical derivation; and more recently Huber and Crosby (1929) in an extensive study of the avian brain found evidence in support of the view that the striatum functions in part as vicarious cortex. What at the moment excites interest in the Bird's brain is not so much the presence within the striatum of certain components which functionally may have cortical value, but the great size of the striatum and the speculation as to how much of it has an origin other than basal.

In the brain of the adult *Sphenodon* the evident continuity of the hypopallium with the cortex is a striking feature as first pointed out by Elliot Smith. There is, however, in the adult avian brain no such evident connection between the cortex and any striatal element, although several writers, including Elliot Smith, Kappers, and Huber and Crosby, have suggested the possibility of such a relationship. The present study has therefore been undertaken to investigate the development of the avian brain as to the origin of the striatal components, and also to ascertain the reason for the departure of the avian brain from the reptilian and mammalian types.

MATERIAL

Numerous brains of the common sparrow (*Passer domesticus*) were sectioned serially for the purpose of this study. The sections, cut transversely at 20μ, were stained by Huber's toluidin blue method (Huber, 1927). On the basis of the developmental stage the brains were then grouped in the following manner:

Stage A, one embryo, head length 5 mm.
Stage B, two embryos, head lengths 7 mm.
Stage C, three embryos, head lengths 8, 8·5 and 8·5 mm.
Stage D, two embryos, head lengths 9·5 and 10·4 mm.
Stage E, one embryo, head length 14·5 mm.

The last stage was sufficiently far developed to be comparable with the adult avian brains described by Huber and Crosby (1929), so that the major striatal components could be followed through from their first appearance to the adult state.

In the earliest stage examined (stage A) a simple undifferentiated condition is found. The ventricular cavity is large and the walls thin. No features are present to suggest future differentiation beyond a slightly greater thickness of the lateral wall of the hemisphere; this, however, is not localised to a particular part of the wall. The cells form a dense layer around the ventricular cavity, leaving a marginal zone of the wall free of cells.

In stage B several changes have occurred and the primordia of several striatal components are apparent. In a section some distance rostral to the foramen of Monro (fig. 1) several areas of proliferation are seen in the ventrolateral wall. The most dorsal projection, forming the primordium of both hyperstriatum and neostriatum, appears most rostrally of all and retains its identity almost to the caudal pole of the hemisphere. It is again shown in fig. 2, where it will be seen to have shifted medially and so become more truly an intraventricular ridge. This movement medialwards of the primordium of the neostriatum and the hyperstriatum is associated with an active proliferation of the cells comprising it.

There is a marked difference in the cells of the lateral wall in different regions. The larger darkly stained cells of the dorsal wall are continued into the lateral wall and occupy the region opposite the swelling which represents the primordium of the neostriatum and the hyperstriatum. Below this level (fig. 2) the wall contains two obvious elements: close to the ependyma is a zone of cells quite indistinguishable from, and continuous with, the neo-hyperstriatal primordium above, while lateral to this the wall is occupied by a second group of cells of different size and staining reactions.

The more ventral projections do not extend so far rostrally as the one described above, but they are larger and show a tendency to fuse when traced caudally. In fig. 1 two such projections are figured; some few sections further caudally a thin ridge projects between them but fuses with them quite soon.

Much of the ventro-lateral wall is occupied by the fore-brain bundle which appears and increases *pari passu* with the general increase in thickness of the wall. The neo-palaeostriatal groove which marks the junction of these elements on their ventricular aspect is at this stage quite conspicuous.

Numerous blood vessels may be seen in the striatum, but no clear evidence of any invariable relationship between blood vessels and striatal masses is present. Particular care has been exercised to find whether any arteries constantly entered at the interval between the neostriatum and palaeostriatum, but no such regularity of pattern can be demonstrated.

By the next stage (C) a very considerable increase in the thickness of the wall has occurred, particularly in the ventro-lateral quadrant. Further, the identity of the various components of the striatum is much more obvious and

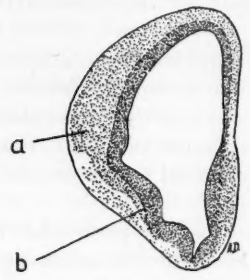

Fig. 1

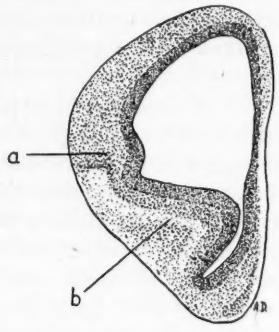

Fig. 2

Fig. 1. Transverse section, left hemisphere. Stage B. *a*, primordium of hyperstriatum and neostriatum. *b*, primordium of palaeostriatum.

Fig. 2. Transverse section, left hemisphere. Stage B. Caudal to fig. 1. Lettering as in fig. 1.

their relationship towards one another commences to show the features distinctive of the adult. The projection (*a* in the figures) which was clearly evident in the previous stage is now larger and forms a more conspicuous swelling. It no longer appears as a mere thickening of the lateral wall but as a striatal mass with which the cortex of the dorsal wall becomes continuous around the dorso-lateral angle of the ventricle and which continues ventrally, close to the ependyma, into the remainder of the striatum. Its lateral part is demarcated from the more ventrally placed masses by a well-defined lamina medullaris externa (figs. 3, 4). This lamina is best marked towards the pial aspect where in many sections blood vessels are found entering the brain wall. It extends medially in a less well-defined manner towards, but fails to reach, the neo-palaeostriatal groove on the ventricular aspect. The cells above and below the lamina are, as in stage B, sufficiently characteristic to make the distinction quite definite.

Dorsal to the lamina the hyperstriatum and the neostriatum can be distinguished. The former consists of densely packed cells adjacent to the

ependyma and derived from proliferation in that region. The neostriatum, placed ventral to the hyperstriatum, consists of larger cells less densely arranged and continuous around the dorso-lateral angle of the ventricle with the more superficial cells of the dorsal wall. The deeper cells in the latter region

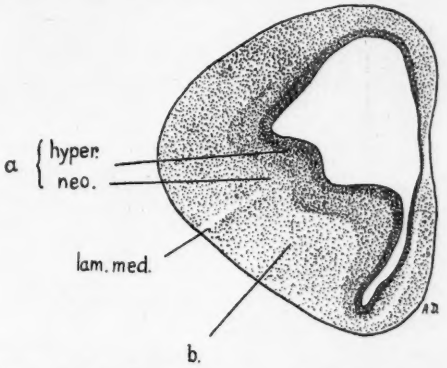

Fig. 3. Transverse section, left hemisphere. Stage C. *a*, the primordium of hyperstriatum and neostriatum which was not clearly divisible in stage B can now be differentiated into hyperstriatum (*hyper.*) and neostriatum (*neo.*). *b*, palaeostriatum. *lam. med.*, lamina medullaris externa vel dorsalis.

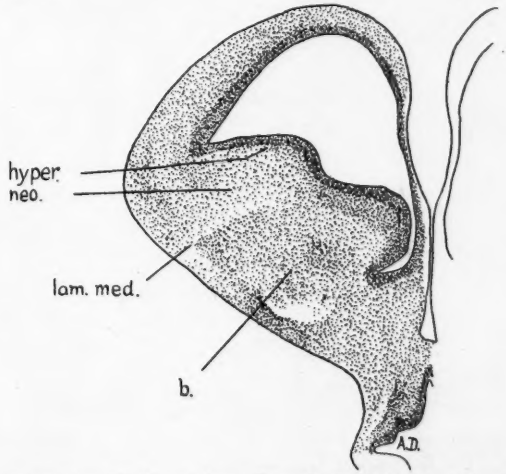

Fig. 4. Transverse section, left hemisphere. Stage C. Caudal to fig. 3. *b*, palaeostriatum. *hyper.*, hyperstriatum. *lam. med.*, lamina medullaris. *neo.*, neostriatum.

are produced by proliferation from the periependymal layer and are continuous with the hyperstriatum. Between the hyperstriatum and the neostriatum no sharp line of demarcation can be drawn; both merge uninterruptedly with the cortex of the dorsal wall. Whether one or both of these entities, the hyper-

striatum and neostriatum, can be produced from the cortex by proliferation or direct extension is a matter which will be discussed later, but in passing one may note that the hyperstriatum and the neostriatum appear to be produced by proliferation *in situ* rather than by any direct extension from the cortex.

The region ventral to the lamina medullaris (figs. 3, 4) is occupied by the palaeostriatum which at this stage shows little evidence of its future subdivision into palaeostriatum primitivum and palaeostriatum augmentatum. Some larger cells occupying the core of the mass and lying in the midst of the fore-brain bundle doubtless correspond with the future palaeostriatum primitivum. The archistriatum cannot as yet be defined with certainty.

In stage D rapid cell proliferation has rendered the whole striatum more bulky, particularly in the dorso-lateral segment of the hemisphere where the

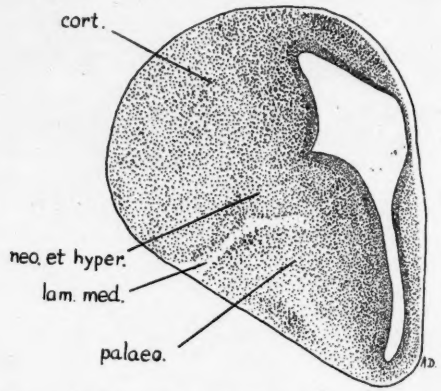

Fig. 5. Transverse section, left hemisphere. Stage D. *cort.*, area of cortical proliferation. *lam. med.*, lamina medullaris. *neo. et hyper.*, neostriatum and hyperstriatum. *palaeo.*, palaeostriatum.

hyperstriatum and the neostriatum are developing. More ventrally the growth of the palaeostriatum proceeds at a slower rate. A section through the rostral part of the hemisphere (fig. 5) shows two main groups of cells separated by a ventricular groove. The more ventral represents the fused masses which were present at this level as individual projections in stage C (figs. 3, 4). The more dorsal projection is the result of the great expansion of the cortical masses in the dorso-lateral region of the hemisphere. This process was already well advanced in stage C (fig. 3), but now becomes a conspicuous feature of the rostral region of the hemisphere. When followed caudally the great cortical thickening does not persist, but gradually becomes reduced to a condition comparable with that of the cortex more medially (fig. 6).

The neostriatum and hyperstriatum show no essential difference beyond an increase in size. Within the palaeostriatum two components are now evident, the palaeostriatum primitivum and the palaeostriatum augmentatum.

The archistriatum occupies the caudal and ventral region of the hemisphere and already consists of cells which in comparison with those of the adjacent palaeostriatum are distinctively large.

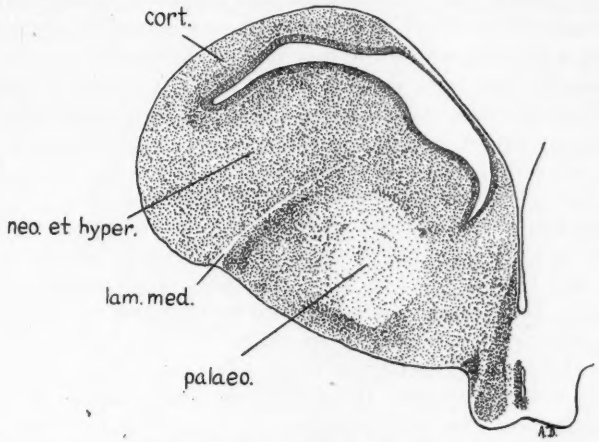

Fig. 6. Transverse section, left hemisphere. Stage D. Caudal to fig. 5. Lettering as for fig. 5.

DISCUSSION

The evolutionary stage from Reptile to Mammal is characterised by the development of a thin cortex cerebri; the total amount of cortex is gradually increased, but this increase is always by further surface extension and not by increase in thickness. In the Bird, however, certain deviations from this trend of cerebral evolution have occurred, so that in the adult avian brain the salient characteristics of both Reptile and Mammal have been very largely obscured by specialisations in the mode of development. The explanation of such specialisation in structure can no doubt be associated with the functional requirements of the Bird. Herrick (1921) has noted that hemispheres with solid cerebral masses as opposed to those with thin sheets of cells have a high efficiency on a reflex plane; "this structural form is correlated with the predominance of stable, heritable, reflex and instinctive behaviour patterns." Mammals exhibiting individually modifiable behaviour and adaptability have the correlation tissue of the brain spread out as thin cortical sheets. It would appear then that one factor in the specialised mode of development of the avian brain has been not so much a reduction in cortex or cortically derived elements as the development of as much of the hemisphere as possible to subserve a life which is carried on predominantly on a reflex plane.

It was in this sense that Kappers (1921) regarded the hyperstriatum as vicarious cortex. In the present investigation it is clear that the neostriatum is also very largely if not entirely of the same derivation as the hyperstriatum,

even though the latter is of later development. It has not been found possible to correlate these striatal elements with the various cortical sheets as in the Reptile. In *Sphenodon* (Cairney, 1926; Durward, 1930) the general cortex and the pyriform cortex was each associated with a separate hypopallial field. The most one can say of the Bird is that both the hyperstriatum and the neostriatum correspond genetically with the hypopallium of the Reptile and that they are related laterally with cortical fields. It is frequently assumed (Elliot Smith, 1919; Johnston, 1923), and has indeed become almost axiomatic, that the hypopallium is formed by ingrowth of the lateral margin of the cortex or by migration of cortical cells from this region, but such a conception is open to dispute. It has been pointed out earlier that the *anlage* of both neostriatum and hyperstriatum is a localised thickening of the lateral brain wall. From this thickening by a process of cell proliferation the ingrowth extends towards the ventricle and ultimately forms the great mass of the hyperstriatum and neostriatum. These masses are not formed by migration or extension of any already existing cortical sheet, but are produced *in situ* by the multiplication of cells in the dense periependymal layers. In a study of the development of the hemispheres in *Sphenodon*, Hines (1923) describes a similar process, and in discussing the derivation of the striatum she says, "this derivation cannot be spoken of as cortical, unless all the tissue which forms the striatum over and above its most ancient components...be of cortical origin." It therefore seems more expedient to regard such parts of the striatum as are commonly accounted of cortical origin as new components which only secondarily acquire an apparent genetic relationship with the contiguous cortical fields. This need not, however, invalidate the view that such striatal elements may have a cortical value functionally.

Considerable interest has attached to those arteries which penetrate the brain wall along the line of the endorhinal fissure, such as the lateral striate arteries so evident in the adult *Sphenodon*. In the latter they undoubtedly do correspond fairly closely with the boundary between the neostriatum and the palaeostriatum, and Elliot Smith discusses their significance in various forms where they maintain this relationship. Kappers (1922) and Hunter (1923) have noted the corresponding vessels in Birds in which the lateral striate arteries penetrate the striatum along the line of the lamina medullaris externa, i.e. along the boundary line between the neostriatum and the palaeostriatum. In the present study these same vessels appear early and increase in size coincidently with the striatal ingrowth towards the ventricle. Other vessels also grow in, but not along the line of any well-defined fibre lamina such as the lamina medullaris and therefore not with the same regularity as the lateral striate vessels. The latter, penetrating at the region of maximal cell proliferation, and coursing along a fibre lamina, acquire a size and regularity which is apt to give them an exaggerated significance, for other vessels are not only numerous but frequently quite large and lack merely the regularity of distribution possessed by the lateral striate vessels. The lateral striate vessels are,

however, constant, and this gives them some significance as a landmark in judging the homologies of the striatal components.

SUMMARY

1. The main stages in the development of the avian striatum have been investigated and briefly described.

2. The hyperstriatum and the neostriatum appear before any differentiation of the palaeostriatum has occurred; their growth proceeds at a greater rate than that of any other sector of the hemisphere.

3. The possible cortical origin of the hyperstriatum and neostriatum has been investigated and the conclusion reached that in the Bird these striatal components bear no genetic relationship to the cortex as such, but are the result of proliferation *in situ* from the dense periependymal layer of cells. It is, however, agreed that these striatal masses may function as vicarious cortex, a view expressed in the past by Elliot Smith, Kappers, and Huber and Crosby. The mode of development is such as to favour the highly reflex behaviour of the Bird and to prohibit the adaptability and the modifiable behaviour characteristic of forms possessing a thin laminated cortex.

4. From an early stage an ingrowth of blood vessels occurs opposite the region of maximal striatal proliferation, along the line of the lamina medullaris dorsalis. It marks the junction between the neostriatum and the palaeostriatum; but other vessels of considerable size penetrate the brain wall in the region of the developing striatum and lack only the regularity of arrangement which characterises the lateral striate group.

ACKNOWLEDGMENTS

I would express my thanks to Profs. Elliot Smith and H. A. Harris of University College, London, for suggesting the study and for advice, and to Prof. J. P. Hill for material. I am also indebted to Prof. MacKinnon of King's College, London, who kindly gave me facilities for examining series of developing *Sphenodon* brains belonging to the collection of the late Prof. A. Dendy.

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THE POSITION OF THE NUTRIENT FORAMEN AND DIRECTION OF THE NUTRIENT CANAL IN THE LONG BONES OF THE MADDER-FED PIG

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INTRODUCTION

The external opening of the nutrient canal, usually referred to as the nutrient foramen, has a particular position and the canal a certain direction constant for each bone. Because of confusion of these two points in the literature on the subject, I wish to stress the fact that the position of the foramen and the direction of the canal are two distinct and separate phenomena of the nutrient artery, and may be the result of independent mechanisms. The literature available is small in amount, deals mainly with direction of the canal, and gives the impression that investigators have assumed that both phenomena are caused by this direction. In this account the position of the nutrient foramen and the direction of the canal will be dealt with separately. Throughout this paper use has been made of the data contained in two previous papers on the growth of the diaphyses and epiphyses of the long bones in the madder-fed pig (1, 2).

MATERIAL AND METHODS

Observations and measurements are made from the limb bones of a dozen madder-fed pigs used in my recent publication on diaphysial growth (1). The age of the pigs varied from 80 to 587 days. These pigs had been treated by the "indirect madder method," whereby the madder is withheld for a period before killing, and consequently the new bone of this non-madder period shows up white against a background of maddered bone. Particulars of age, madder period and non-madder period are noted in Table I.

Table I. *Duration in days with and without madder feeding.*

Pig No.	Age at death days	Madder period days	Non-madder period days
14	80	72	8
15	91	77	14
16	108	84	24
17	126	105	21
12	140	61	28
1	169	68	29
2	197	97	28
3	225	125	28
4	279	153	54
6	362	207	84
9	475	271	126
8	587	394	116

Longitudinal sections were cut through the long axes of the diaphyses and the plane of the section was chosen to pass through the nutrient foramen.

HISTORY

Bérard (3), almost 100 years ago, noticed that the direction of the nutrient canals in the human being was constant for a given bone. He noticed that in the upper limb the canals were directed towards the elbow and in the lower limb away from the knee. He advanced no theories concerning these observations, but remarked that the nutrient artery entering the bone divided into two branches, ascending and descending, the branch continuing in the direction of the main artery was the larger, and therefore, because of the better blood supply, caused union to occur first of all between the diaphysis and epiphysis towards which it flows. Thus the canal is slanted towards that end at which the epiphysis is first united to the shaft.

In this series of pig bones the direction of the nutrient canal has been noted and this is considered with regard to the end of the diaphysis which first unites with its epiphysis (Table II).

Table II. *The direction of the nutrient canal in relation to the end of the diaphysis which unites with its epiphysis first.*

In humerus canal	directed	away from	distal	end of diaphysis	which unites	with its epiphysis first
„ radius	„	towards	proximal	„	„	„
„ ulna	„	towards	proximal	„	„	„
„ femur	„	away from	proximal	„	„	„
„ tibia	„	towards	distal	„	„	„
„ fibula	„	towards	distal	„	„	„

It is to be noted from Table II that for the bones of the pig the humerus and femur disagree with Bérard's statement.

In contrast with Bérard's idea, Humphry (4) demonstrated, by means of madder staining in the pig's bones, the unequal growth of the two ends of the diaphysis, and stated that the obliquity of the canal was not the cause but the effect of the unequal growth. This unequal growth at the two ends would cause an unequal drag on the periosteum which is fixed to the two ends of the bone. Humphry's dragging theory is disputed by Piollet (5), who states that in the human foetus the nutrient arteries are directed first perpendicularly to the bone's long axis and then later all proceed distally in the bone, while still later the arteries of the radius, ulna and femur change their direction, so that in the adult all the arteries are found directed away from the growing ends as the result of unequal growth of the diaphysis in which growth is peripheral, while growth of soft parts is interstitial. Thus both Humphry and Piollet associate the obliquity of the nutrient canal with the unequal growth of the diaphysis.

In Table III the direction of the canal in respect to the greater growing end of the diaphysis is noted for this series of bones.

Table III. *To show the relation between the direction of the nutrient canal and the end of the diaphysis with the greater growth.*

In humerus	canal	directed	proximally	and	proximal	end of diaphysis	is greater growing end
„ radius	„		proximally	„	distal	„	„
„ ulna	„		proximally	„	distal	„	„
„ femur	„		distally	„	distal	„	„
„ tibia	„		distally	„	proximal	„	„
„ fibula	„		distally	„	proximal	„	„

It is seen from Table III that the nutrient canals in the pig's humerus and femur are directed towards the end of the diaphysis with the greater growth, in contrast to Piollet's and Humphry's statements.

Various authors, in addition to the foregoing, have supported (6) or disagreed (7) with these statements without, however, adding to our knowledge.

The text-books of anatomy generally quote either Bérard's (8) or Humphry's and Piollet's (9) theories. A few of them remark that the reason for the obliquity seems obscure.

Since the nutrient canals as observed in the long bones of the pig do not agree with any of the above theories, is it just possible that this apparent agreement for the human long bones is one of mere coincidence?

GENERAL OBSERVATIONS

In the pig's humerus the nutrient foramen is situated on the posterior surface near the junction of the middle and distal thirds of the shaft. The canal is directed proximally into the bone. The outer end of the canal comes into relation with the lower edge of a layer of new bone which is being laid down on the exterior of the posterior part of the shaft (fig. 1).

It will be noticed that the nutrient canal of the *humerus* does not enter the shaft so obliquely as is the case in the other bones, because the canal is involved in a modelling process at the distal end of the diaphysis. It has been shown (1) that new bone is added to the distal end of the diaphysis and that most of this new bone is rapidly absorbed on the anterior and posterior aspects of this extremity to form the coronoid and olecranon fossae. Owing to the distal extremity growing downwards and forwards the olecranon fossa becomes the deeper of the two fossae and requires to be filled in on its proximal aspect to enable the shaft of the humerus to extend in a distal direction. Consequently a layer of new bone is found on the posterior part of the olecranon fossa extending proximally on the posterior surface of the shaft as far as the nutrient foramen. In this way the nutrient foramen is sandwiched between two edges of new bone—one, the distal edge of new bone added to the shaft, and the other, the proximal edge of new bone added to the olecranon fossa. This peculiar position of the canal between two layers of new bone in addition to lessening the obliquity of the canal may also modify any movement of the canal in respect to the layer of new bone round the shaft; but reference to this point is made later.

In the *radius* the nutrient foramen is situated on the posterior surface of the shaft near the junction of the proximal and middle thirds. The canal is

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Figs. 1–6 are respectively longitudinal sections cut through the nutrient canals of humeral, radial, ulnar, femoral, tibial and fibular diaphyses of Pig. No. 4. Age 279 days. The areas of bone unstained by madder are represented white and indicate new bone laid down during the non-madder period of 54 days. Bone stained by madder is black or stippled.

directed proximally into the bone. The external end of the canal lies at the lower edge of new bone which is being added to the outside of the posterior part of the shaft (fig. 2).

In the *ulna* the nutrient foramen is situated on the anterior surface of the shaft near the middle. The canal is directed proximally into the bone. The inner end of the canal lies in relation to the upper margin of new bone which is being added to the inside of the anterior part of the shaft (fig. 3).

In the *femur* the nutrient foramen is situated on the anterior surface of the shaft near the junction of the proximal and middle thirds. The canal is directed distally into the bone. The outer end of the canal lies in relation to the proximal margin of new bone which is being added to the outside of the shaft (fig. 4).

In the *tibia* the nutrient foramen is situated on the posterior surface of the shaft near the junction of the proximal and middle thirds. The canal is directed distally into the bone. The outer end of the canal lies in relation to the proximal margin of new bone which is being added to the outside of the shaft (fig. 5).

In the *fibula* the nutrient foramen is situated on the medial surface near the junction of the proximal and middle thirds. The canal is directed distally into the bone. The outer end of the canal lies in relation to the proximal margin of new bone which is being added to the outside of the shaft (fig. 6).

Position

It is generally agreed that the vessels which occupy the nutrient canal are derived from those that took part in the initial invasion of the ossifying cartilage, so that the nutrient foramen was at the site of the original centre of ossification. It is known that the diaphysis increases in length unequally at its two ends, so that it is not surprising to find the foramen nearer one end of the diaphysis. But when it is found that the position of the foramen bears no mechanical relation to the growing ends of the diaphysis a problem is raised. The following observations go to show that the canal moves independently of the growth in length of the diaphysis.

Observations of the appearance of the bone immediately surrounding the foramen and especially of the appearance of sections through the foramen show that absorption is taking place on one side and addition of new bone on the other. These observations are noted for all the long bones in Table IV.

Table IV. *To show the position of absorption and addition of bone round the nutrient foramen.*

In humerus	absorption occurs on the	distal*	and addition on the	proximal	side of foramen
„ radius	„	distal	„	proximal	„
„ ulna	„	distal	„	proximal	„
„ femur	„	proximal	„	distal	„
„ tibia	„	proximal	„	distal	„
„ fibula	„	proximal	„	distal	„

* This absorption is slight for humerus, as explained on p. 502.

This observation gives an indication that the foramen may move independently of the growth of the diaphysis.

Further support of this independent movement could be obtained if a landmark on some bone from which measurements could be taken could be shown to remain stationary so far as diaphysial increments are concerned. Such a guide was found on the ulna, in which bone the proximal articular surface is carried by the diaphysis. On this articular surface is a groove dividing the sigmoid notch into olecranon and coronoid parts. The following calculations show that the groove is constant in position so far as growth in a proximal and distal direction is concerned.

Measurements from this groove to the proximal end of the diaphysis in a young and an old bone give the following results: No. 14 (80 days old), 28 mm., No. 9 (475 days old), 42·5 mm. This gives an increase in the length of this section of the ulna of 14·5 mm. in No. 9 which is 395 days older than No. 14.

Now the amount of new bone added to the proximal end of the diaphysis can be measured by means of the madder staining. These measurements have already been published.

From these measurements it is seen that the upper end of the diaphysis grows in relation to the lower end as 0·5 : 1·0. The length of No. 14 diaphysis is 100 mm. as compared with No. 9 which is 143 mm. Therefore No. 9 is 43 mm. longer than No. 14. The upper end of the diaphysis adds one-third of this, namely 14·3 mm. Thus it is apparent that only the proximal end of the section of bone grows and that the groove in the sigmoid notch remains stationary, so far as alteration in a proximo-distal direction is concerned.

Measurements have been made of the distance between this groove on the sigmoid notch of the ulna and the nutrient foramen (Table V).

Table V. *Measurements of distance between groove on sigmoid notch of ulna and nutrient foramen.*

	Measurements in mm.									
Ulna No.	14	15	16	17	12	1	2	3	4	6
Age (days)	80	91	108	126	140	169	197	225	279	362
Distance, groove to foramen	25·5	27·5	28·7	27·0	31·0	27·5	27·0	36·0	33·3	35·5

From these measurements it is seen that the foramen travels distally as one passes from the younger to the older bones.

Further evidence of the independent movement of the nutrient foramen can be got by measuring the distance between the nutrient foramen and the proximal end of the diaphysis (Table VI) and using these measurements to mark the position of the nutrient foramen on the graphs (already published) where the diaphyses are in such a position that they can be superimposed so far as growth in length is concerned (figs. 7, 8).

If the older theories that the position of the foramen was dependent upon unequal growth of the diaphysis held good these foramina should be in a horizontal line on the graphs, and should be situated in that half of the bone

Table VI. *Measurements in mm. of the distance between the nutrient foramina and the proximal end of the diaphyses.*

	Pig No.											
	14	15	16	17	12	1	2	3	4	6	9	8
Humerus	58·0	60·0	50·3	68·8	70·5	70·2	76·0	80·5	84·2	79·0	85·3	100·2
Radius	16·5	20·5	21·0	20·2	28·7	20·0	25·0	30·2	34·0	23·2	29·0	32·3
Ulna	55·3	58·1	58·3	60·0	65·0	62·0	70·0	80·5	75·8	75·0	80·2	100·0
Femur	34·2	30·5	35·1	38·6	35·0	34·0	35·0	38·2	38·0	43·2	40·3	47·2
Tibia	38·0	38·0	44·0	50·0	47·7	47·0	54·0	60·4	54·3	60·2	62·0	70·3
Fibula	46·0	40·0	28·5	40·0	40·8	44·5	40·5	48·0	55·6	55·0	42·3	66·2

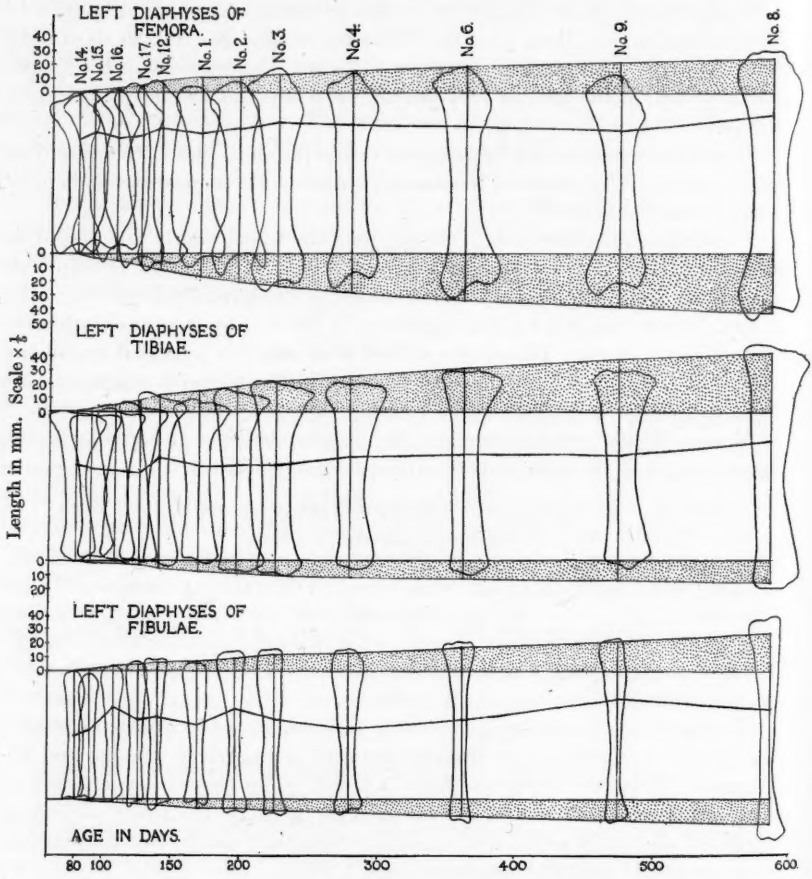

Fig. 7. Graphic representation of the relative rates and amounts of growth at the ends of the humeral, radial and ulnar diaphyses as previously published(1), with the position of the nutrient foramina indicated as explained in the text.

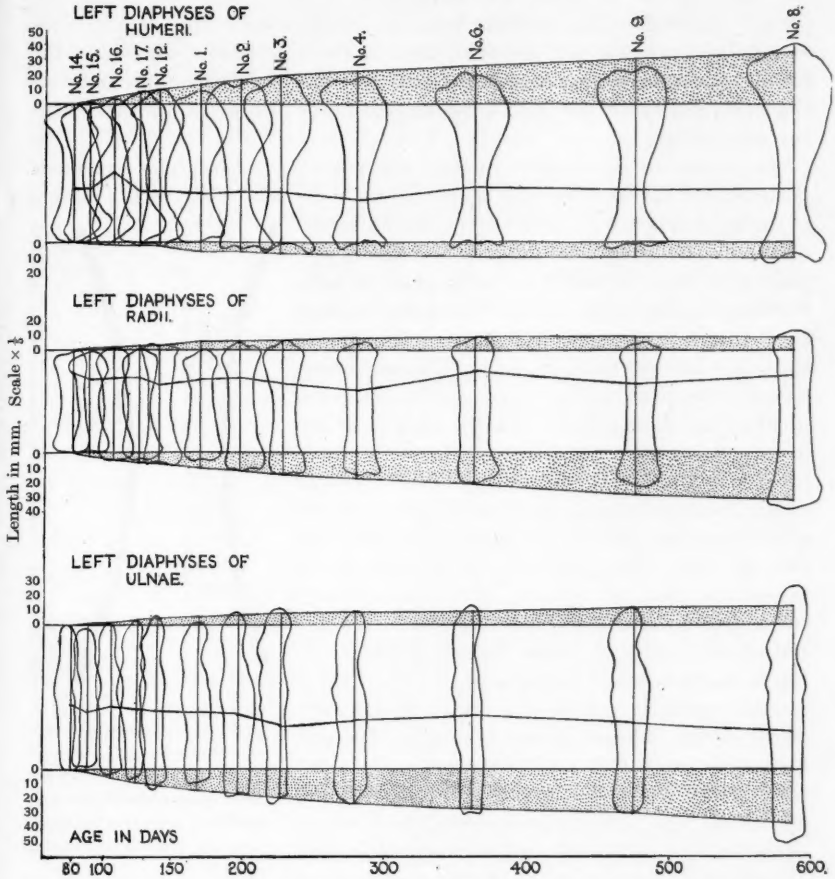

Fig. 8. Graphic representation of the relative rates and amounts of growth at the ends of the femoral, tibial and fibular diaphyses as previously published(1), with the position of the nutrient foramina indicated as explained in the text.

remote from the end with the greater increment. It is seen, however, that in none of the graphs except the humerus are the foramina in a horizontal line. Further, the foramina of the ulna, tibia and fibula are situated in that half of the bone with the greater increment. It is also observed that the foramina of these last-mentioned bones move towards the end with the greater increment as the age of the bones increases. The exception of the humerus has already been anticipated (p. 502) owing to the peculiar position of the canal which is situated between two layers of new bone which would tend to keep it stationary.

Direction

The direction of the nutrient canal is constant for a given adult bone. It has been pointed out, however, that in the case of the pig bones, the direction bears no constant relationship to the epiphysis which unites first with the shaft, nor is the direction a mechanical result of unequal growth at the two extremities.

By means of the madder method the following observations are made possible: the nutrient foramen is seen to enter the shaft close to the margin of the band of new bone added to the circumference of the diaphysis, for the purpose of keeping this part of the bone in proportion to the growing ends. Further, in some of the younger bones this nutrient canal is seen to enter the medullary cavity close to the oldest part of the shaft. In the majority of the bones, if the canal is at the upper end of the bone, it enters the shaft proximodistally, while if at the lower end, it enters in the reverse direction, disto-proximally. At whichever end of the shaft the canal enters it will be found to run parallel to the nearest edge of new bone which is being added to the shaft (fig. 9). This holds good with all the long bones except the ulna, the foramen of which is exactly the reverse in direction, i.e. it lies near the upper end of the bone and enters disto-proximally. In this bone, however, it can be seen that the shaft is convex anteriorly and shows no layer of new bone on the surface. A longitudinal section (fig. 3) through the anterior wall of the shaft of this bone shows that the layer of new bone added to the shaft is being deposited on the internal surface, and the direction of the bevel at the upper and lower ends of this band of new bone is the reverse of that met with in the other long bones. At the upper end the bevel slopes upwards and inwards and at the lower end downwards and inwards (fig. 10). The nutrient canal of the ulna is parallel with the bevel at the upper end and runs upwards into the bone.

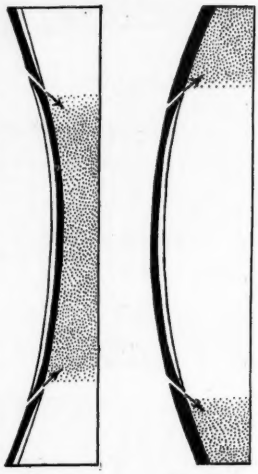

Fig. 9. Fig. 10.

Figs. 9 and 10 respectively show the directions which the nutrient canal may take when new bone is added to the outer and inner aspects of the shaft; the new bone is represented white.

The band of new bone round the shaft of the diaphysis is regarded as secondary to the growth at the ends of the diaphysis (1). It keeps the thickness of the shaft in proportion to the size of the diaphysial ends. The growth of the diaphysial ends slows down with the age of the bone, so the band of new bone round the shaft requires to extend less at its margins and the margins become less acute. Now if the nutrient canal bears relationship to the margin of new bone, a change in the obliquity of the canal will occur with the age of the bone.

The actual degree of obliquity of the nutrient canal has been measured in all the tibiae of the series by the following method: A line is taken through the middle of the maximum side to side diameter of each end of the diaphysis. A straight wire rod is inserted into the nutrient canal and the angle is measured between this wire and the first line (fig. 11). The measurements of the angles thus obtained are set out in Table VII.

Table VII. *Measurements of the angles between the long axis and nutrient canal of tibiae as described in the text.*

Pig No.	14	15	16	17	12	1	2	3	4
Angle	16°	17°	17·5°	18°	17°	17·5°	20°	19°	20·5°

Fig. 11. To show the method of measuring the angle between the planes of the nutrient canal and the long axis of the diaphysis as described in the text.

The angle is observed to increase with the age of the bone, and the greater this angle the less oblique is the nutrient canal to the long axis of the bone.

SUMMARY AND CONCLUSIONS

The position of the nutrient foramen bears no relationship to the unequal growth at the diaphysial ends—it has actually been shown to approach the diaphysial extremity with the greater increment in some bones.

There is a considerable amount of evidence that the foramen moves independently of diaphysial growth as shown by:

(1) observations of absorption and addition of bone round the margins of the nutrient foramen;

(2) measurements from a fixed point on the ulna indicating that the nutrient foramen travels distally with the increasing age of the bone;

(3) the position of the nutrient foramen (plotted upon graphs in which the diaphyses can be superimposed) moving with the age of the bone, except in the case of the humerus, for which an explanation is given.

The direction of the nutrient canal is not dependent upon the union of epiphyses or the unequal growth at the diaphysial extremities. It is shown that the canal follows the bevel of the edge of new bone added to the shaft. The bevel at the end of this new bone becomes blunt as the general rate of growth slows with age, and correspondingly the nutrient canal decreases in obliquity. This decrease in obliquity is not accompanied by a shortening, but by an increase in length, because, as pointed out previously (1), the absorption generally on the inside of the shaft does not balance the addition generally on the outside, a process resulting in an increase in the thickness of the wall of the shaft.

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A COMPARISON OF THE JOINTS OF THE ARM AND LEG AND THE SIGNIFICANCE OF THE STRUCTURAL DIFFERENCES BETWEEN THEM

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The work embodied in this paper commenced in an attempt to find an explanation of the many differences in structure between the elbow- and knee-joints in Man. The arm and leg are built on a common plan and in most respects closely resemble each other. Consequently the difference in the structure of the joints is the more remarkable.

The difference can be explained in part by the fact that the bones of the fore-arm have retained the movements of pronation and supination, while in the leg the bones are almost immovably fixed together. A further part of the difference can be explained by the fact that the ulna, or post-axial bone, preponderates at the elbow, but the tibia, or pre-axial bone, preponderates at the knee. Parsons has shown (1) that in the Reptiles the great extensor muscle of the fore-limb is inserted into the ulna, but in the leg the corresponding muscle is inserted into the tibia. This apparently led to the difference in the bones which predominate at these two joints. In the Mammals the limbs have departed from the reptilian position and have been turned in under the body, the two limbs rotating in opposite directions during this process. The limbs have then become supporting as well as propelling organs. In the leg the tibia carries the foot and is placed on the medial side of the limb, that is the side best fitted for supporting the weight of the body; in the fore-arm the radius carries the "hand," and by pronation of the "hand" is also placed on the medial side of the limb. Thus in many quadrupeds the tibia and radius come to preponderate in the leg and fore-arm respectively; the fibula often disappears completely, but the upper end of the ulna into which the extensor muscle is inserted always persists, its persistence has been determined by the insertion of this muscle. This prominence of the ulna at the elbow-joint leads to considerable difference between that joint and the knee.

There is, however, one matter of contrast between the joints which cannot be wholly explained by these facts; namely that the ulna at the elbow projects as the olecranon above the level of the joint and interlocks with the trochlea of the humerus, whereas the tibia at the knee has no upward projection and in consequence there is no interlocking of the bones. The ulna cannot be compared morphologically with the tibia, but, as stated above, the great extensor muscles of the two limbs are inserted into these bones and therefore they are comparable functionally.

The presence of the olecranon is associated to some extent with the freedom of movement between the bones of the fore-arm, for it fixes the ulna as regards rotation and therefore assists it to act as a base for the movements of pronation and supination of the hand. As, however, a well-developed olecranon is found in animals which have lost the power of supinating the hand, it must serve some other function. It is this other function of the olecranon which has to be defined.

The greatest development of the olecranon is found in the highly specialised quadrupedal Mammals, the Carnivora and the Ungulata. In them the olecranon is one of several similar features in the limbs. The skeleton of each limb consists of three segments, the adjacent segments meeting one another at an angle. In the fore-limb the humerus passes downwards and backwards; the radio-ulna passes downwards and slightly forwards, or sometimes, especially in the standing posture of the animal, straight downwards; and the carpus is

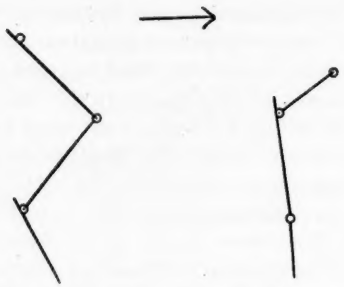

Fig. 1. Diagram of limbs of a typical quadruped. Arrow points in direction of animal's head. Note that segments meet each other at an angle and that the upper end of segments which slope downwards and forwards is prolonged up above articulations in which they take part.

usually aligned with the radio-ulna or inclines slightly backwards in digitigrade animals and straight forwards in plantigrade animals. In the hind-limb the femur passes downwards and forwards, the tibia downwards and backwards, and the tarsus downwards and forwards (see fig. 1). In each limb, therefore, the bones pass downwards and forwards or downwards and backwards, and the corresponding segments in the two limbs pass in different directions. In both limbs, with the exception of the carpus which is very short, the upper ends of the bones which pass downwards and forwards are prolonged above the level of the articulations in which they take part. Thus in the femur the great trochanter is prolonged above the level of the hip; in the tarsus the calcaneus is prolonged above the ankle, and in the radio-ulna the olecranon projects above the level of the elbow. In these quadrupeds therefore the great trochanter at the hip-joint and the posterior projection of the calcaneus at the ankle-joint are features similar to the projection of the olecranon at the elbow; and if any functional significance can be ascribed to the great development of the

olecranon in these animals then the same significance will apply to the upward projection of the great trochanter and the posterior end of the calcaneus.

When such an animal moves forwards it does so by pushing backwards on the ground with its hind-feet, and first pulling and then pushing backwards with its fore-feet. These actions are, by the resistance of the ground, converted into a forward motion of the animal's body. The various segments of the limbs are levers by which the animal brings about these stresses and, as the feet are fixed on the ground, the lower ends of the segments are the fulcra of the levers. In the case of the upper segments of each limb the lower end of the segment is not absolutely fixed, for it is not on the ground, but it is fixed relatively to the upper end. The weight bears on these levers at the centre of the articulations at their upper ends.

In the case of those segments which pass downwards and backwards, fixation of their lower ends and movement of their upper ends around this fixed point will not produce any forward movement of the animal, or at most can only produce a movement downwards and slightly forwards. But at each step the animal requires a forward and upward impulse, the upward element being necessary to balance the force of gravity while the foot is off the ground and the limb is being brought forwards preparatory to another step. But in the case of those segments of the limbs which pass downwards and forwards, movement of their upper ends around their fixed lower ends will obviously produce a forward and upward impulse to the animal's body. Accordingly, Mivart (2) recognised that the tarsus is the lever mainly concerned in forward movement in the cat, and Huxley (3) recognised the same fact as regards Man. It appears therefore that the bones in the limbs which are aligned in a downwards and forwards direction are the levers by which an animal moves forwards.

As already stated all of these bones are prolonged up above the articulations at their upper ends, and the extensor muscle by which the power is applied to the lever is inserted into the extreme upper end of the prolongation. The bones are therefore levers of the second order in which the weight is between the power and the fulcrum. The mechanical advantage of such a lever is obtained by dividing the total length of the lever from power to fulcrum by the distance from the weight to the fulcrum. It is evident, therefore, that the upward prolongation of these bones confers a mechanical advantage on the extensor muscles when an animal is propelling itself forwards.

Figs. 2 and 3 show the actual conditions found at the ankle- and elbow-joints in quadrupeds. Figs. 4 and 5 show the conditions as they would be if the tarsus and radio-ulna did not project up above these joints. In this last case if the feet were on the ground and the animal were propelling itself forwards the tarsus and radio-ulna would still be levers of the second order, but the points of application of the power and of the weight would approximately coincide and no mechanical advantage would accrue. For it should be noted that the lower end of the extensor muscles is composed of non-contractile tendon, and the point of application of the power is not at the insertion of the

muscle but at the place where the tendon passes round the upper end of either the tarsus or the radio-ulna.

The mechanism of the lower limb in Man when he is moving forwards is very similar to that of the hind-limb in quadrupeds during the same action. Keith (4), Hooton (5) and Huxley (3) all recognise that the foot is a lever of the second order, and that the backward projection of the calcaneus adds to the

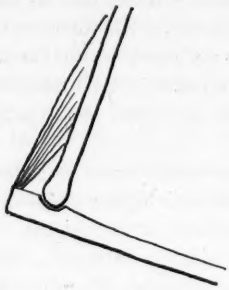

Fig. 2.

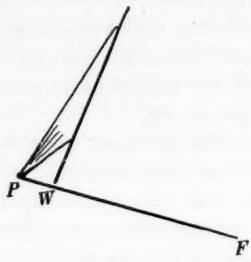

Fig. 3.

Fig. 2. Plan of condition which is actually found at elbow- and ankle-joints of a quadruped.

Fig. 3. Plan to show that radio-ulna and tarsus are levers of the second order when the animal's feet are on the ground and these bones are used to propel the animal forwards.

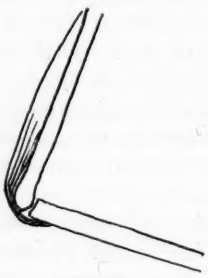

Fig. 4.

Fig. 5.

Fig. 4. Plan showing conditions as they would be at the elbow- and ankle-joints of a quadruped if the radio-ulna and tarsus did not project upwards above these joints.

Fig. 5. Plan showing that conditions shown in fig. 4 would still be a lever of the second order if the feet are on the ground and the limbs are used to propel the animal forwards.

power of the muscles of the calf. Keith (4) points out that there are some races with a long calcaneus and slender calf muscles, and others with a short calcaneus and therefore bulky calf muscles.

If we now consider movement of the tarsus and radio-ulna when the feet are off the ground and the lower ends of these bones are free to move we will find that the upward projections also in this case add to the power of the extensor muscles but in a different manner to the former case. The weight is

now approximately at the lower end of the bones; the power is applied at the insertion of the muscles, and the fulcrum is at the articulation at the upper end. As the fulcrum is between the power and the weight the lever is one of the first order, and the mechanical advantage of such a lever is found by dividing the distance from the fulcrum to the power by the distance from the fulcrum to the weight. Obviously, as in this case, the former distance considerably exceeds the latter there is no mechanical gain from the lever; there is in fact a loss of power but a gain of speed. If the upper ends of these bones did not project, the muscle tendon would have to be placed somewhat as is shown in fig. 4, that is, it would pass round the back of the joint and be inserted into the upper and posterior surface of the bone. The point of application of the power would still be at the insertion, but, as this point is now between the weight and the fulcrum, the lever is one of the third order. In levers of the third order the mechanical advantage is obtained, as in the other orders, by dividing the distance from the power to the fulcrum by the distance from the weight to the fulcrum, and in this case again there would obviously be a loss of power but a gain in speed. This, of course, is always the case with levers of the third order. As far as leverage is concerned, therefore, the advantages of these two arrangements would appear to be about equal, and no benefit arises from the fact that the bones do project up above the joints. But in the second case, that is, when the bones would be acting as levers of the third order, the extensor tendon would lie nearly parallel to the axis of the bone. The force exerted by this tendon can be resolved into two components, one in the line of the axis of the bone which has no power to move it but can only compress it against the bone above, and the other at right angles to the axis which is the effective component in moving the bone. As the tendon would be almost parallel to the axis its component in the line of the axis would be much greater than its component at right angles to it, and the power of the muscle would be considerably wasted. But in the first case, that is, in the actual conditions which exist in the quadrupeds, the tendon lies almost at right angles to the axis of the bone, and consequently the whole of the power of the muscle is available to move it. The upward projections of the tarsus and radio-ulna therefore ensure that the tendons of the extensor muscles are inserted approximately at right angles to the axes of the bones and therefore increase the power of these muscles to move the bones on the articulations at their upper ends.

The olecranon, the upward projection of the calcaneus and, to a lesser degree, the great trochanter of the femur therefore can be seen to have a considerable functional significance in the quadrupeds; they increase very considerably the power of the extensor muscles when the feet are on the ground, and these bones are used as levers of the second order to propel the animal forwards, and they also increase the power of the muscles when the feet are free and the bones are moved on the articulations at their upper ends.

It should be remarked that two of the levers which produce forward movement of the body are situated in the hind-limb, but only one in the fore-

limb. This accords with the known fact that it is the hind-limb which imparts the greater part of the impulse to propel the animal. It is also noteworthy that the upward projection of the femur is not so marked as the similar projections of the radio-ulna and tarsus. This apparently is due to the fact that the femur is very close to the body wall and therefore muscles can pass from the pelvis to the shaft or lower end of the bone and be inserted at a favourable angle. These muscles can exert a great force on the femur, and the need for an upward projection of the bone to give the muscles a favourable angle of insertion is not so urgent. But as the radio-ulna and calcaneus are at a distance from the body and as the limbs cannot become too bulky the muscles which operate on these bones are compelled to pass down close to and almost parallel to the axis of the limb. They therefore would have to be inserted at a very unfavourable angle if the radio-ulna and calcaneus were not prolonged upwards.

If an animal moves backwards it does so by using the segments of the limbs which pass in the opposite direction, that is, downwards and backwards, as levers of the second order in the same manner as it used the other segments to obtain forward movement. But animals rarely move backwards, and the ability to do so rapidly and forcibly is not of much advantage to them. So we find that the upper ends of the levers concerned in backward movement are not modified in the same way that is found in those concerned in forward movement. Thus the upper ends of the humerus and tibia-fibula are not prolonged upwards[1].

In the quadrupeds the olecranon and upward projection of the calcaneus are adaptations for a definite purpose. What has happened to these processes in animals which have abandoned a quadrupedal gait?

As regards the upward projection of the calcaneus, Hooton (5) gives the following observations for the Primates:

Man	Large	(A terrestrial biped)
Baboon	Large	(A terrestrial quadruped)
Gorilla	Medium	(A brachiating ape but lives largely on the ground)
Chimpanzee	Short	(A brachiating ape)
Orang-utan	Shorter	(A more specialised brachiating ape)
Gibbon	Shortest	(The most highly specialised brachiating form)

The remarks in brackets in this table are mine. It will be noticed that the length of the calcaneus varies inversely as the arm-length to body-length ratio,

[1] In some animals, especially those inhabiting rough and broken ground, e.g. goats, sheep, and deer, the greater tuberosity of the humerus does form an upward projection of this bone above the shoulder-joint. Owing to the rough ground they inhabit such animals have often to raise the front end of the body vertically upwards in order to surmount some obstacle, and this has often to be done from a standing position. The animal accomplishes this movement by pushing downwards and slightly forwards with its fore-legs. The humerus is therefore used as a lever of the second order to propel the front end of the body upwards and slightly backwards. Hence the increased leverage of this bone furnished by the projection.

in other words the more a brachiating habit of life is adopted the greater is the retrogression of the calcaneus.

Other animals which have ceased to use the hind-limb as an organ of terrestrial propulsion furnish similar evidence. Thus in the bats the posterior end of the calcaneus does not project backwards but is turned downwards. These animals when resting suspend themselves by their hind-limbs, and the downward turned tuberosity of the calcaneus is admirably suited to flex the soles of the feet towards each other when the creature is hanging by its feet from a branch. It thus may be regarded as an adaptation for this peculiar mode of resting. Among the sloths the tuberosity varies. In *Choloepus* it is short, flattened from side to side, and its lower edge projects downwards, thus approaching the condition found in the bats. In *Bradypus* it is long, but the flattening from side to side and the turning down of its lower edge are still evident.

From the above facts it seems clear that in those animals which have ceased to use the hind-limb as an organ of propulsion the posterior projection of the calcaneus has been modified to a greater or less degree. In the opposite direction we may notice the great development of this projection in the saltatory animals. It seems evident therefore that this projection is a lever developed in terrestrial quadrupeds or bipeds and adapted for propelling the animal forwards.

Similar evidence seems to apply in the case of the olecranon of the ulna. In the specialised quadrupeds it is always large. In those animals which have ceased to use the fore-limbs as organs of propulsion it has almost invariably been modified. It is absent in the bats. In the kangaroos, wallabies and sloths it is small. In the jerboas it is rather large, but these animals are possibly quadrupeds when feeding or traversing short distances. In the brachiating apes it is small. Man occupies a position between the lower apes and the anthropoids. Martin (6) gives the following figures for the height of the upper surface of the olecranon in the Primates:

Gorilla	0·8	Australian	1·8
Gibbon	1·0	Negro	1·9
Orang-utan	1·1	Fuegian	2·5
Chimpanzee	1·4	Neanderthal	4·7
European	1·7	Lower apes	6·4
Melanesian	1·7	Lemurs	8·3

The above figures are obtained by making a true outline of the upper end of the ulna at right angles to the plane of the central ridge of the greater sigmoid cavity. The axis of the upper end of the bone is drawn on this outline, and a perpendicular to the axis is drawn from the tip of the olecranon. The maximum distance from the upper surface of the olecranon to this perpendicular is then measured and expressed as a percentage of the physiological length of the ulna.

From this table certain facts are evident. First, that in the higher races of

Man the olecranon is gradually disappearing. Secondly, that in the anthropoids it has already disappeared to a greater extent than in Man. Thirdly, among the anthropoids the extent to which the olecranon has diminished is, with the exception of the gorilla, directly in proportion to the extent to which brachiating habits have been adopted. In face of these facts it seems difficult to avoid the conclusion that the olecranon was first developed to serve as a lever for the extensor muscles of the fore-limb in quadrupedal animals, and therefore to increase the efficiency of these muscles in propelling the animal forwards. Subsequently, in those animals that have abandoned quadrupedal methods of progression the olecranon has retrogressed.

If the above views are correct it would appear that the extent to which the upper ends of the femur, tarsus and ulna project in Man should furnish some evidence as to his ancestry, and as to the particular line of development by which his ancestors were gradually modified. For these projections are all adaptation for the use of the limbs as terrestrial propelling organs. Man still uses his legs for this purpose but he has ceased so to use his arms. It is easy therefore to account for these features in his lower limbs. For when his ancestors descended from the trees and became terrestrial bipeds the posterior projection of the calcaneus still served as the main lever for propelling his body forwards and therefore would be conserved or even increased, and as regards the great trochanter, though with Man's upright attitude it lost its usefulness as a lever for propelling the body forwards, yet it became a very convenient insertion point for the abductors and rotators of the thigh. The size of Man's calcaneus would suggest, however, that his ancestors descended from the trees before the development of brachiating habits had led to its retrogression, otherwise it must have secondarily reincreased.

The relatively large olecranon in Man, on the other hand, is not so easily explained unless it is accepted as a heritage from his quadrupedal, or semi-quadrupedal ancestors. It should be noted that all the lower apes are semi-quadrupedal in gait even in their arboreal habits. Morton (7) uses the expression "pronograde apes" to distinguish them from the orthograde brachiating anthropoids. The size of Man's olecranon then suggests that his ancestors came from a race of semi-quadrupedal apes with well-developed olecrana, and they must have become terrestrial before brachiating aboreal habits led to its retrogression to such a marked extent as we see in the anthropoids.

But once Man's ancestors had adopted a terrestrial mode of life they became implement users, and then certain factors would tend to conserve the olecranon. For in such actions as striking downwards with a hammer, club or sword, or hurling a javelin, rapid and forcible extension of the fore-arm is essential, and earlier in this paper it was pointed out that the presence of the olecranon not only added to the power of the extensor muscles when the arm was used as a propelling limb but also increases the power of these muscles when the ulna is extended on the humerus. The olecranon therefore would be useful in the performance of these acts and its atrophy would

thereby be at least delayed. This perhaps explains the large olecranon of Neanderthal Man as he is generally depicted wielding an enormous club. But in modern races with their universal machinery it is slowly disappearing.

Morton (7) gives a summary of several different lines of evidence on the question of Man's ancestry and concludes that he and the modern anthropoids had a common ancestor, but that the pre-human stock diverged from the pre-anthropoid one before the latter developed marked specialisations for a brachiating and arboreal life. The evidence furnished by the olecranon appears to confirm his conclusions and constitutes an additional and independent piece of evidence which has not hitherto been adduced.

The reason why the human knee-joint is so unlike the elbow-joint is that the two limbs rotated in opposite directions when the transition from the reptilian to the mammalian stage was taking place. This led to the corresponding segments in the two limbs sloping in different directions, for the uppermost segment of each had to slope towards the other so as to bring the limb as nearly as possible under the centre of gravity of the body. Those segments which sloped downwards and forwards became the levers for propelling the animal forwards, and owing to the importance of this movement their upper ends became prolonged upwards to give increased efficiency in this movement. The other segments of the limbs remained unmodified. In the quadrupeds therefore the elbow-joint is mechanically equivalent to the ankle-joint, and the knee to the wrist. The two former are at the upper end of a lever concerned in forward progression; the two latter are not so situated. Therefore the knee- and wrist-joints are in many respects very similar in structure, and the elbow- and ankle-joints also closely resemble each other.

Some other points of contrast between the two limbs in Man can be explained if the above facts are borne in mind. Thus the tarsus is rather long and the separate bones are firmly fixed together, while the carpus is short and the bones loosely attached. Again, the distal articular surface in the ankle-joint is composed of a single bone, but the similar surface at the wrist is composed of three bones. But as the tarsus is one of the levers concerned in forward progression, it is obviously advantageous to make it unyielding, to give it a reasonable length in order to acquire speed, and to make the point where the weight bears on it—that is at the ankle-joint—as rigid as possible. But these influences have not operated at the carpus, for it did not become a lever much concerned with forward progression, even in the plantigrade animals where it passes forwards, apparently because it is situated at the lower end of a bone which slopes downwards and forwards in the quadrupeds, and therefore it had a poor purchase for pushing the body weight forwards.

Further, before the common ancestors of Man and the anthropoids had taken to an arboreal life, the two limbs had already rotated. For such a life it is necessary that the palms of the hands and the soles of the feet should be able to turn inwards so as to face each other. In the case of the hands this ability is obtained by retaining the power of supination, but in the case of the feet as

the legs had rotated in the opposite direction to the arms, retention of the power to pronate would result in turning the soles of the feet outwards. So we find that the ability to pronate the hind-limb has been lost, but at the mid-tarsal joint the power to invert the foot has been developed. In the Primates, then, inversion of the feet becomes the mechanical equivalent of supination, or partial supination of the hands.

CONCLUSIONS

Many of the structural differences which exist between the human knee- and elbow-joint, and between the ankle- and wrist-joints are due to the fact that Man is descended from a quadrupedal, or semi-quadrupedal arboreal type. The olecranon especially bears witness to Man's semi-quadruped ancestors. The evidence suggests that Man's ancestors abandoned the trees and became terrestrial bipeds before the brachiating specialisations which are so evident in the anthropoids began to develop. The evidence from these joints therefore confirms the conclusions drawn by Morton and other workers from evidence supplied by other anatomical features.

I desire to express my thanks to Prof. Walmsley of Queen's University, Belfast, for the loan of much literature, and for many helpful suggestions in the writing of this paper.

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CERVICAL INTERCOSTAL ARTICULATION

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Both personal familiarity with a considerable amount of anomalous cervical vertebral material and a review of the relevant literature suggest that the case herein briefly described presents a condition of parts sufficiently rare as to justify its record. The case manifests an adventitious and additional articulation between the third and fourth cervical vertebrae through the medium of a diarthrosis developed between the anterior tubercles of the transverse processes, or, in morphological terminology, through a cervical intercostal articulation. The specimen consists of the third and fourth vertebrae from the cervical spine of an adult (presumably female) column of continental origin, otherwise normal, and is available through the courtesy of Prof. W. H. Wood, to whom acknowledgment is here made for permission to examine and report upon it. These two vertebrae articulate in the usual manner by both bodies and arches but also additionally, on the left side, by means of the adventitious joint between the highly modified anterior tubercles of their transverse processes. This extra joint lies opposite the intervertebral disc, with its articular plane inclined at an angle of some 30° from the horizontal, and bears every evidence of having been truly diarthrodial. No suspicion of pathological change occurs in the specimen.

(*a*) THE THIRD CERVICAL VERTEBRA

The bone manifests trifling asymmetry. Its left cranio-caudal height is diminished some 2 mm. by reason of the abbreviation and lateral displacement of the left neuro-central apophysis. The left supralaminar notch is deeper than the right, suggesting greater unilateral pressure by the left inferior articular process of the axis vertebra. The virtually non-bifid spinous process is deflected leftwards. With the exception of the left transverse process all parts of the bone are normal and typical in character. This left transverse process, in comparison with its right fellow, is less overhung by its articular pillar, has a thicker posterior limb, a somewhat more bulky posterior tubercle, and a more shallow neural gutter. Its costo-transverse lamella is unduly thick and its anterior limb unusually broad: the anterior tubercle is peculiarly exaggerated into a roughly pyramidal process, 11·0 mm. high by 7·5 mm. broad, projecting antero-inferiorly and bearing upon its inferior aspect an oval facet for articulation with the equally anomalous anterior tubercle of the subjacent vertebra. The vertebrarterial canal and the sulcus nervi spinalis remain unaltered.

(*b*) THE FOURTH CERVICAL VERTEBRA

The right half of this vertebra is typical in all respects. The left and larger of the two bony flanges constituting its spinous process deviates inferolaterally. The left supralaminar notch is deeper than the right but the left articular pillar is normal. Compared with its right fellow, the left transverse process is atypical in the following respects. Its posterior limb is thrice the

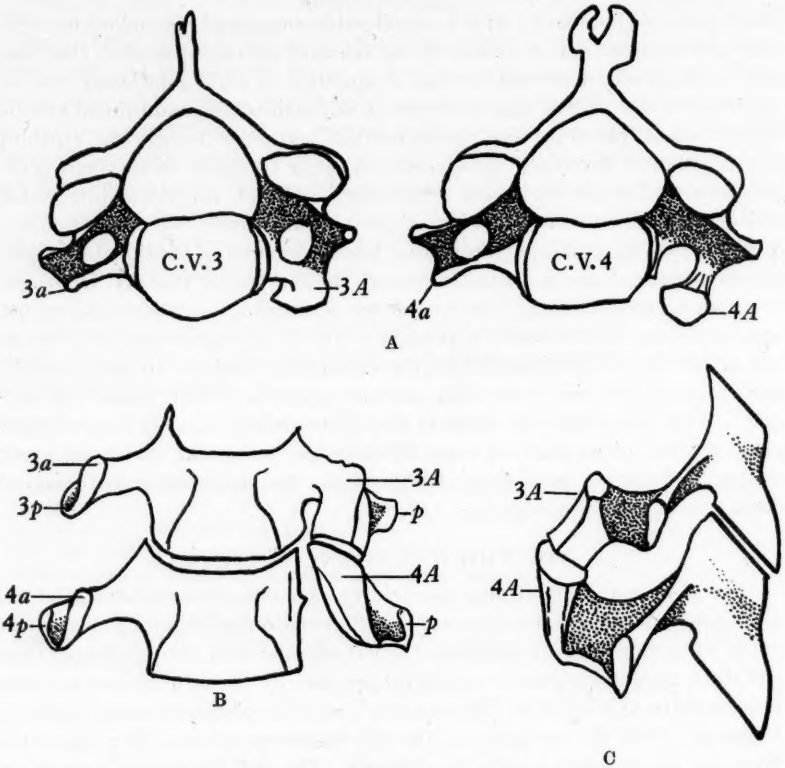

Fig. 1. Cranial (A), anterior (B), and left lateral (C) aspects of third and fourth cervical vertebrae, showing modified anterior tubercles (3*A*, 4*A*), normal anterior (*a*) and posterior (*p*) tubercles, and neural gutters (stippled).

usual thickness and is less recurved in its outer half; its posterior tubercle, essentially unchanged, is somewhat obscured by the undue thickness of the costo-transverse lamella. Anteriorly the floor of the neural gutter rises rapidly into the enormous, misshapen anterior tubercle, an irregular, inverted pyramidal mass, some 13 mm. high by 8 mm. broad above, which projects superomedially from the front of the costo-transverse bar. The oval, sloping superior

aspect of this tubercle, cartilage covered in life, articulates with the corresponding process of the third vertebra. The anterior aspect of the tubercle is flattened by the prevertebral and scalene musculature, the posterior is hollowed by the vertebral artery. The medial moiety of the anterior limb is deficient, but a bony spicule, projecting laterally from the vertebral body towards a medial ridge on the enlarged tubercle, suggests the former closure by ligament of the now open vertebrarterial foramen.

(*c*) GENERAL

Bearing in mind the possible causal influence of the spinal nerves in the production of this anomalous arrangement of parts, radiographic estimation was made of the angle of inclination of these structures to the vertical median axis of the spinal canal, the nerves in question being represented by soft wires in the neural gutters. Inasmuch as the issuing spinal nerve does not necessarily maintain throughout its path its initial plane of emergence from the cord, this method is merely a convenient makeshift; but allowing for its imperfections it did demonstrate that the nerves on the anomalous (left) side pursued a more abruptly caudal slope than their opposite fellows. Thus the third right nerve emerged at an angle of 30°, but its left fellow at one of 40°. The fourth right nerve had an inclination of 40°, but its left fellow a primary inclination only of this order, which rapidly increased to one of 50°. Such increased caudal inclination, however, is totally insufficient to account for contact between the affected transverse processes. Moreover, the anomaly lies wholly anterior to the plane of the nerves, and altogether a primary neural rôle in the production of the variation must be dismissed. Muscle traction and vascular arrangements are equally impracticable as causal agents, and the variation must be classed as an example of defective segmentation of the cervical axial skeleton, essentially a union between the costal elements of the third and fourth segments, with the secondary formation of the intertubercular diarthrosis for the conservation of cervical mobility.

(*d*) COMMENT

The variation is descriptively intercostal, morphologically costal (or pleurapophyseal) in nature. It represents a localised successful manifestation of the inherent tendency of adjacent costal elements (pleurapophyses) to effect intersegmental union whenever possible, and whatever their degree of functional specialisation. This particular faculty for intersegmental union, widespread throughout the vertebral column, constitutes one aspect of pleurapophyseal dominance during vertebral ontogeny. Normally it is obtrusive only in the consolidation of the sacral lateral masses, but as a variant may affect any region of the presacral spine.

Such presacral occurrence is most commonly evidenced in the frequent cases of sacralisation of the fifth lumbar vertebra, but Shore (3) has reported in the Bantu native an adventitious left-sided articulation between the transverse

processes (pleurapophyses) of the third and fourth lumbar vertebrae, which appears from his figure to be morphologically strictly comparable with the present cervical case, whilst Cumming (1) has submitted radiographical evidence of a presumably similar condition of parts in the modern British subject. In the thoracic region pleurapophyseal union may assume one of two forms, a ventral or a dorsal, both associated, perhaps significantly, with a longitudinal disposition of the trunk musculature. The first is exemplified by the fairly frequent diarthrodial connections between two or more costal cartilages (usually the fifth, sixth and seventh) in association with the rectus abdominis muscle: the second is seen in the occasional diarthrodial or synosteal connection between the necks of adjacent ribs, and is associated with the erector spinae system. From the purely lateral aspect of the chest wall such variations are notably absent.

To the same morphological category belong those specimens of cervical rib which either fuse with the first thoracic rib or articulate therewith by means of special eminences developed upon the opposed surfaces of the two bones, whilst at the cranial extremity of the cervical spine must be included all examples of occipito-atlantal articulation through the medium of a paramastoid (paroccipital) process. The intervening cervical region remains singularly free from the occurrence of this type of variation. Apart from the present case but one previous example is known to the writer—that reported in this *Journal* by Grunbaum (2) and involving the sixth and seventh vertebrae. (Grunbaum's morphological interpretation of his specimen is unintelligible, though happily his figure is self-explanatory. The enlarged left anterior tubercle of the sixth cervical is synostosed caudally with the entire pleurapophyseal element of the succeeding vertebra, the latter retaining its appropriate vertebral connection by means of a medial (capitular) and a lateral (costo-transverse) synchondrosis. Little, if any, intervertebral movement was possible.)

An extensive survey of material from many anatomical centres has failed to reveal any further example of this particular variation. The few cases cited above will suffice, however, to emphasise its purely pleurapophyseal nature, its predilection for left-sided occurrence and its close association with a craniocaudal disposition of the musculature, an association doubtless ancillary to its formation.

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THE DEVELOPMENT OF THE EXTERNAL EAR

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FISTULA AURIS CONGENITA

The little pits or fistulae, known by a variety of names, such as helical fistulae, pre-auricular fistulae, etc., which occur in the neighbourhood of the tragus and crus helicis, are probably present as fairly frequent anomalies in all races. In the African Negro of Nyasaland, Stannus (11) found them in 5·2 per cent. of females and 3·6 per cent. of males. Congdon has recently described a large series in Siamese and other races in Bankok (2). They occur (with a frequency of about 2 per 1000, according to Eyle) in the white races all over the world, and they have long been known to be frequent among the Chinese.

Depressions may occur at various sites upon the auricle, but the present authors agree with Ballantyne (1) that the term fistula auris congenita should be restricted to those pits and fistulae that are situated on, or anterior to, the crus helicis. The pit, and the fistulous track that sometimes leads from it, are definitely congenital: at times they are bilateral, but more usually unilateral. In Stannus's African series the occurrence upon both sides was 0·77 per cent., upon the right side alone 2·08 per cent. and upon the left side alone 1·69 per cent. A definite hereditary history is present in most cases. An example was shown at the Royal Society of Medicine by Dr Prichard (quoted by Stannus) in an infant having bilateral fistulae and whose mother, four siblings, maternal grandmother and two great aunts all exhibited the same anomaly.

As to the commonest site of occurrence, it is probable that some clarity of thought has been lost by the recording of small puckers in varying parts of the auricle and regarding them as true pre-auricular fistulae. Stannus has classified the sites in which his 292 observed fistulae occurred into five positions, and these accord so exactly with our own findings that they are here combined into one figure (see fig. 1 A). The line upon which these fistulae occur may be defined as a curve passing from the temple to the anterior margin of the crus helicis and so to the interspace between the crus helicis and the upper part of the tragus; thence into the concha to the external auditory meatus and out again between the lower part of the tragus and the anti-tragus to the skin at the junction of the concha and the skin of the cheek.

Although these fistulae are undoubtedly of congenital origin, there has always been a difficulty in accounting for their formation. Stannus assumed them to be "remains of the first branchial cleft," and such an assumption has

been made by other observers. But it is obvious that their site of election does not occur along the line of closure of the first depression, as that is pictured in the generally accepted account of the development of the external ear. In discussing their origin, Ballantyne came to the conclusion that "there are two difficulties (at least) in the way of a full and free acceptance of this view" (that they are derivatives of the first depression). "The first is the freedom of the middle ear from participation in the deformity, and the other is the position of the fistulae."

Stammers (10) concludes his account of two cases and a review of the literature by saying: "these fistulae are not remnants of the first branchial cleft,

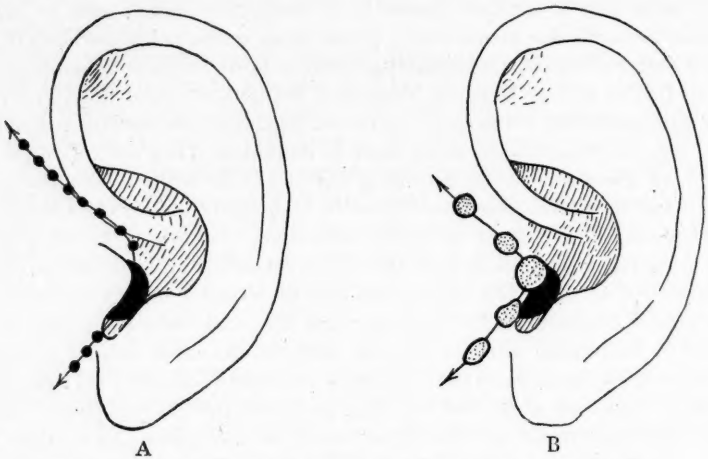

Fig. 1. A. The distribution of pre-auricular fistulae. B. The distribution of pre-auricular appendages.

but result from aberrent coalescence of the six tubercles which are destined to form the pinna." Congdon, in the most recent paper on the subject, considers them to arise from the intertubercular grooves and postulates that shifting of the skin, during the processes of growth, accounts for their general disposition.

There are many difficulties in the way of assuming that these pits and fistulous tracks are caused by faulty union of the so-called auricular tubercles or hillocks of the embryo. In the first place, their distribution by no means appears to follow the lines of union of the several hillocks, as these were depicted by His (7) and later by Streeter (12): and in the second, the hillocks themselves, even as pictured by these investigators, are of such low elevation that it is hardly possible to conceive of a pit or a fistula being formed at their sites of junction.

PRE-AURICULAR APPENDAGES

One point of considerable interest lies in the fact that pre-auricular fistulae are at times complicated by the presence of accessory auricular appendages, as in the cases recorded by Ballantyne and by Congdon, and it is therefore possible that some light may be thrown on their origin from an examination of these appendages.

Pre-auricular appendages (accessory auricles, supernumerary tragus, etc.) are of fairly common occurrence. By Warner they were reported 33 times in the routine examination of 50,000 children. It must not be forgotten that these little skin tags are often removed for cosmetic purposes; but, if bifid tragus be included under this heading, they would appear to have a far higher frequency in the Chinese. Six Chinese foetuses, out of our series of 400 at the Peiping Union Medical College, showed this condition either unilaterally or bilaterally.

The site of pre-auricular appendages appears to be very constant: from the tragus as a centre they may extend upwards and forwards towards the temporal region, between the upper part of the tragus and the crus helicis; or downwards towards the cheek, between the lower part of the tragus and the anti-tragus. It is therefore clear that the line of election of pre-auricular appendages lies just in front of the line of election of pre-auricular fistulae (see fig. 1B). It would certainly seem that this general agreement of the sites of these two anomalous conditions of the auricle argued for a common and normal developmental process underlying them both.

THE DEVELOPMENT OF THE EXTERNAL EAR

Before His published his classical account of the development of the external ear, the descriptions of the process available in the literature were very meagre. Warton Jones's account (8) is difficult to follow and no distinctions are made between the portions of the ear arising from the mandibular arch and those developing from the hyoid. Allen Thomson's work (13) led to some amplification of the descriptive details, and his statement that "the pinna is gradually developed on the posterior margin of the first branchial cleft" remained as the accepted account of the process for thirty years and through successive editions of Quain's *Anatomy*. It would seem that, previous to the description published by His, the pinna was regarded as a hyoid derivative.

According to His's researches, the pinna was developed from three tubercles or hillocks situated on the mandibular arch and three on the hyoid arch. The after history of these hillocks and the respective shares that the mandibular and hyoid hillocks have in the formation of the definitive auricle have been rather variably estimated by a series of later investigators—Gradenigo, Schwalbe, Baum and Dobers, Henneberg, Streeter and others.

The main point of interest, from a morphological point of view, is how much of the definitive external ear is mandibular and how much hyoid in origin.

According to His, the mandibular contribution embraces the tragus, the crus helicis, and the helix itself as far as the tuberculum auriculae. Other investigators have differed from His mainly in defining other limits upon the helix as the termination of the mandibular element. It is at once apparent that the precise determination of the site of junction of hillocks 3 and 4 (or the meeting of mandibular and hyoid elements) is a matter of some importance, since this point must mark the upper limit of the first pharyngeal depression.

If the current account of the development of the external ear be correct, we must assume that the line of the first pharyngeal depression passes upwards and backwards from the incisura intertragica and across the meatus auditorius externus to the region of the tuberculum auriculae (see fig. 2).

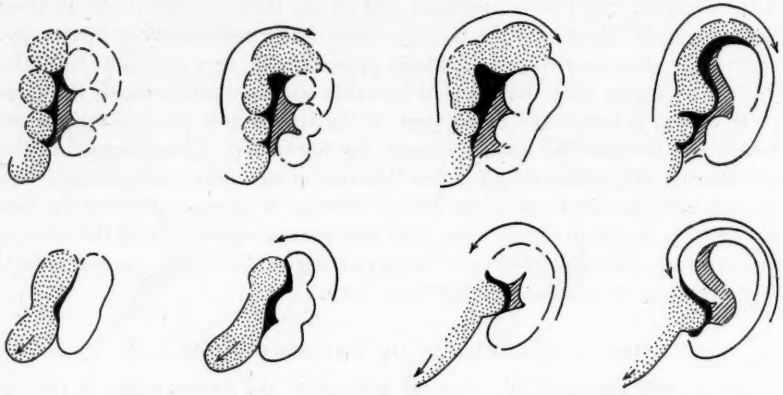

Fig. 2. The development of the external ear. The fate of the mandibular and hyoid elements as depicted by His, etc. (upper series), and as determined in the present investigation (lower series).

It would seem that such a disposition of the first depression is unlikely, since the crus helicis lies definitely behind the meatus or on the hyoid side of the depression. By the classical description a migration of the upper two mandibular tubercles is demanded, the migration taking place in a dorsad and caudad direction so that a considerable portion of the pinna on the hyoid aspect of the meatus is postulated as having shifted from the mandibular side.

In order to test the reality of this migration of the mandibular portion of the pinna, we re-examined the series of embryos in the collection of the Peiping Union Medical College. Our initial difficulty in studying the developing auricle in these well-preserved, formalin-hardened, embryos was the lack of any confidence we felt in identifying the six hillocks that constitute the fundamental features in the classical accounts of the process. This difficulty applied more particularly to the mandibular arch; for upon the hyoid arch it was often possible to detect slight elevations in the caudal boundary of the first depression. Feeling that this inability to detect the hillocks with any real

conviction might be due to our own faulty observation, we gave the series of embryos to the departmental Chinese artist, with instructions to produce enlarged drawings of exactly what he could see in the neck region. The latter's drawings of a series of embryos ranging from 12 to 24 mm. coincided exactly with our own observations and differed widely from the classical figures given by His, but they very strikingly resembled those which illustrate Frazer's work (see especially *J. Anat.* vol. LXI, pp. 132–43). It is possible that this discrepancy is accounted for by the method of preservation, and that shrinkage in spirit may render these hillocks more apparent, or may even determine their presence. It would appear that others have had difficulty in identifying the hillocks and in following their transitions, for Keibel (9) states, "I have not been able to get a clear picture from the investigation of the human embryos at my disposal, but it seems certain that the tragus is developed from the first auricular hillock and the antitragus from the sixth, and that the auricular lobe is a later formation that has nothing to do with the hillocks."

It is apparent, from the first stage at which the rudiments of the auricle are visible, and throughout the whole of the subsequent stages, that the elevation on the hyoid arch is far more extensive and far more prominent than is that on the mandibular arch. It is also apparent that the mandibular portion is growing forwards (ventrad) on the anterior aspect of the first depression as the prominence of the chin region begins to develop upon the growing jaw. Such a movement would seem to indicate that, if there be any translation of the hillocks from one side of the depression to the other (as is postulated on the classical description), it would be evidenced by the higher hyoid hillocks (Nos. 4 and 5 of His) passing round the upper margin of the depression, rather than in a migration of the upper mandibular hillocks (Nos. 2 and 3 of His) to the hyoid aspect of the depression. The process of development, as it appears to be demonstrated in our series of embryos, appears to consist in the formation of a raised margin upon the hyoid boundary of the first depression. This elevation presents a somewhat tuberculated appearance at certain stages and these tubercles might perhaps justify the name of hillocks: but we agree with Keibel that "the investigation of the further history of these structures is unusually difficult." The difficulty appears to arise from the inconstancy of the hillocks themselves. The hyoid elevation differentiates into an auricular fold before any structural landmarks are apparent upon the mandibular elevation. The hyoid auricular fold extends beyond the most dorsal limit of the first pharyngeal depression, and soon encircles the upper end of the depression. This movement appears to be consequent upon the forward growth of the mandible. The mandibular boundary of the depression now shows a definite elevation, which in some specimens shows evidence of partial subdivision into tubercles. At the junction of the hyoid auricular fold and the upper part of the mandibular elevation an inflection takes place and the hyoid portion curves down so that it sweeps in and forms the crus helicis, which however never succeeds in passing to the mandibular aspect of the depression, but distorts the upper part

of the depression in its growth. In this way the mandibular elevation is depressed and persists as the definitive tragus. It would seem from the figures given by Frazer ((4) p. 139, fig. 7) that the process here described is exactly the same as that seen by him when making his drawings, for the whole of the auricle, with the exception of the tragus, appears to be formed from the hyoid elevation.

In fig. 2 (lower series) we have endeavoured to show the processes as we conceive them to take place contrasted with those invoked in the classical description. It may appear to be a retrograde step, but we conclude that Allen Thomson's observation ("the pinna is gradually developed on the posterior margin of the first branchial cleft") made in 1844 is not far from the truth. The tragus appears to be the only mandibular derivative of the pinna and the line of the first pharyngeal depression appears to coincide with the line of election of pre-auricular fistulae.

THE EXTERNAL EAR IN CASES OF ARRESTED DEVELOPMENT OF THE MANDIBULAR ARCH

A very large number of cases of failure of the mandibular arch to be fully developed are recorded in the literature. Failure of development may express itself over a wide range of malformations, ranging from trivial degrees of micrognathia to complete agnathia. These anomalies occur in lower animals as well as in man, and the peculiar frequency of an agnathic condition in lambs is well known to sheep breeders. Although associated malformations of the pinna have been reported in certain human cases, they are by no means a necessary concomitant of the primary malformation, nor indeed are they its usual accompaniment.

The typical condition seen in cases of agnathia is for the whole of the pinna to be developed behind the meatus auditorius externus;—but the tragus is entirely unrepresented. A very complete case of agnathia is that described by Hannover 50 years ago (6). Two malformed auditory ossicles and three minute spicules of bone alone represented the mandibular arch; and yet only the tragus was missing from the external ear. Hannover's original illustration is reproduced here as fig. 3. Another case, which duplicates that of Hannover in almost every detail, is that described by Graham (5) and in this case also the external ear was complete with the exception of the tragus. In a specimen examined for the purposes of the present inquiry (Melb. Univ. Path. Mus. No. 62A) the region of the first arch had already been dissected and all traces of it are said, on the label, to have been absent. The external ear of this specimen is illustrated at fig. 4. The tragus is absent, but with that exception the external ear is well developed, save that the lobule is not well defined and is adherent. These examples are typical of the condition, and it would therefore seem to be a definite fact that absence, or almost total absence of the first pharyngeal arch, involves no more deformity of the external ear than the lack

of development of the tragus. The helix being well developed in cases of agnathia, would certainly seem to indicate that it was not formed from the mandibular arch.

THE NERVE SUPPLY OF THE EXTERNAL EAR

There is a marked discrepancy between the nerve supply of the pinna as determined by anatomists and that commonly recognised by the clinician. The anterior auricular branches of the auriculo-temporal nerve are accepted, in the standard anatomical descriptions, as supplying the front of the upper part of the auricle. The area of supply by the trigeminus is usually depicted as including the whole of the upper part of the pinna down to about its mid-point on the posterior margin, sometimes including the tragus (Quain) and sometimes

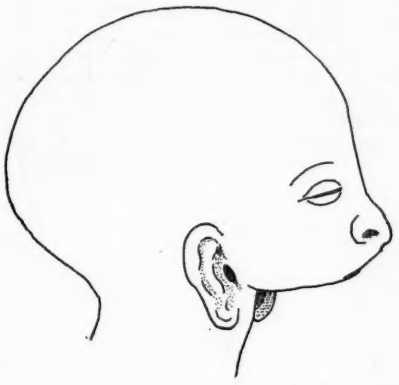

Fig. 3. The external ear in Agnathia. Hannover's case, 1884.

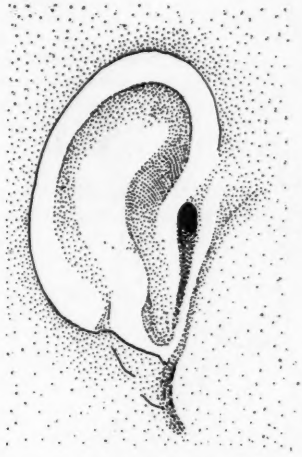

Fig. 4. The external ear in Agnathia. Melbourne University Path. Mus. No. 62A.

omitting it (Gray) in front (see fig. 5A). Nevertheless, although at the present day there seems to be a general agreement among anatomists that the auriculotemporal nerve supplies a large part of the pinna, this has not always been the accepted opinion. Macalister, in 1889, described the auricular branch as being "lost on the skin of the tragus and vicinity of the intertragic notch"—a description almost identical with that of Holden (1861), Knox (1853), Ledwick (1852) and other nineteenth century anatomists. There is no doubt that this earlier description is adequate for a great many cases; in others, branches, apparently from the auriculotemporal, may be traced to the upper part of the pinna. It is, of course, likely that the actual distribution of the cutaneous nerves supplied by this branch of the trigeminus varies within fairly wide limits: but it is also likely that, in many cases, the branches identified in gross

dissection are actually those of the nervus facialis that are running with the trigeminus. The great interchange of fibres between the trigeminus and the facialis has taken place before the anterior auricular branches are given off from the former. In some cases, even by gross methods, it can be demonstrated that the auricular branch proceeding to the top of the pinna is destined for the supply of m. helicis major. In lower Mammals (such as *Macropus*) it is obvious that, whilst the auricular branches of the facialis pass up to supply the muscles of the large pinna, the auricular branch of the trigeminus goes no farther than

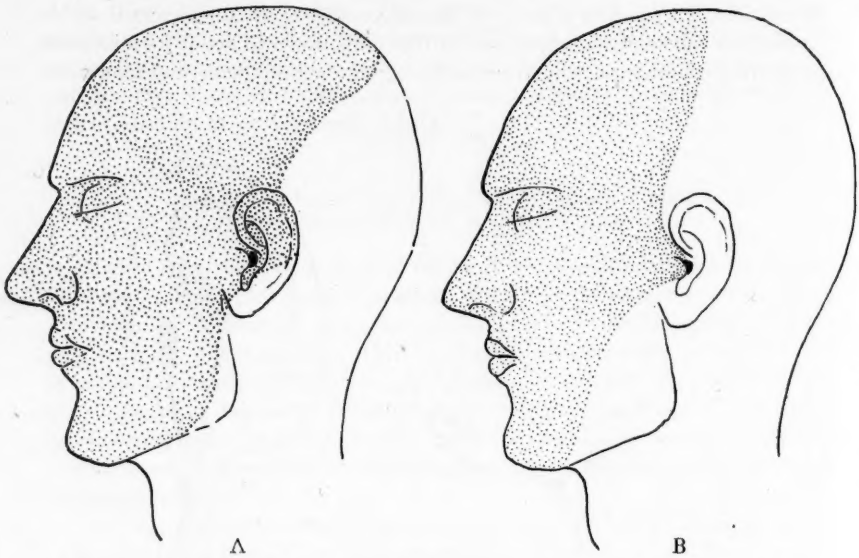

Fig. 5. The distribution of the trigeminus to the ear (A) according to most anatomists (after Thane); (B) according to most clinicians (after Foerster, Head and Cushing).

to the front of the external auditory meatus. It is, therefore, highly probable that the true supply of the auricular branch of the trigeminus passes no farther on to the pinna than the tragus and the anterior aspect of the external auditory meatus as Macalister affirmed.

In neuritis of the trigeminus the pinna itself is not painful; and, conversely, after removal of the Gasserian ganglion or section of the third division of the trigeminus the anaesthetic area does not invade the pinna. There is now very definite agreement among clinicians that the trigeminus supply is limited to the tragus and to the anterior part of the external auditory meatus (see fig. 5B). On the other hand, section of the great auricular nerve produces anaesthesia of the whole of the pinna with the exception of the anterior part of the external auditory meatus and the tragus.

CONCLUSION

It appears from the study of the development, anomalies, and nerve supply of the external ear, that the pinna is a hyoid derivative and that the mandibular contribution is represented only by the tragus and the anterior part of the external auditory meatus. It is, therefore, evident that pre-auricular fistulae and pre-auricular appendages do, in reality, lie along the line of the first pharyngeal depression.

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A COMPARATIVE STUDY OF THE ANTERIOR CEREBRAL ARTERY AND THE CIRCLE OF WILLIS IN PRIMATES

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I. INTRODUCTION

In attempting to approach the hypothalamus of monkeys by transection of the corpus callosum, the anterior cerebral artery proved to be a source of unexpected difficulty (Watts and Fulton, 1934). While retracting the vessel laterally to pass an instrument between it and the falx cerebri, branches were seen passing from the single arterial trunk to both hemispheres. Examination of the brains of other specimens of this species of monkey (*Macaca mulatta*) showed that each anterior cerebral artery runs antero-medially toward the longitudinal fissure of the cerebrum, where it joins its fellow to form a single trunk which passes forward into the fissure. Within the fissure the anterior cerebral artery lies close to the rostrum and body of the corpus callosum, and sends cortical branches to the medial surfaces of both hemispheres. This led to a systematic examination of the anterior cerebral artery and circle of Willis in all available Primate brains, and the results of the study are recorded in the present paper.

The earliest description of the cerebral blood vessels of a subhuman Primate which could be found in the literature is by Tyson (1699). This author made a careful study of the anatomy of a chimpanzee which he erroneously designated as an "orang-utan" or alternatively as a "pigmie." Of the structures on the base of the brain he wrote[1]:

"...On the *basis* of the *Brain*, we may view all the *Ten pair* of *Nerves* exactly situated and placed as in a *Humane Brain*; nor did I find their Originations different, or any Particularity that was so. I shall therefore refer to the *figures* I have caused to be made of the *Brain*, and their Descriptions; where we may observe the *Arteriae Carotides*, *Vertebrales*, and *Communicans*, and the whole of the *Blood Vessels* in our *Pygmie* to be the same as in a Man."

The first observations on the distribution of the anterior cerebral artery of the subhuman Primates which could be found were by Theile (1852). This author, in a study of the entire arterial system of four specimens of *Simia inuus*, refers to the anterior, middle, and posterior cerebral arteries and the

[1] Tyson (1699), see p. 56.

posterior communicating artery. Of the anterior cerebral artery which he calls the *arteria corporis callosi* he wrote:

"Sie wendet sich nach vorwärts und einwärts in die Spalte zwischen den beiden vordern Hirnlappen, und hier fliessen die rechte und linke Arterie zu einem unpaaren Aste zusammen, ohne aber an Dicke zuzunehmen. Diese gemeingeschäftliche Art. corporis callosi verläuft zwischen den beiden vordern Hirnlappen nach vorwärts, biegt sich über das Balkenknie nach oben und hinten und versorgt beide vordern Hirnlappen, so wie den Balken."

An unusual opportunity for making a comparative study of the cerebral arteries presented itself, because of the large number of Primates used for experimental purposes in this laboratory. Some of the specimens were examined in the fresh state but the majority after fixation in formalin or alcohol. The arachnoid was dissected away and the blood vessels studied *in situ*.

II. MATERIAL[1]

	No. of brains examined
Family PONGIDAE, the anthropoid apes	
Genus *Pongo*	
Pongo pygmaeus, orang-utan	4
Genus *Pan*	
Pan satyrus, chimpanzee	6
Family HYLOBATIDAE, the lesser apes	
Genus *Hylobates*	
Hylobates lar (*H. leuciscus*), lar gibbon ...	1
Hylobates hoolock, hoolock gibbon	1
Family CERCOPITHECIDAE, the Old World monkeys	
Genus *Cercopithecus*	
Cercopithecus sabeus, green monkey	19
Genus *Erythrocebus*	
Erythrocebus patas, patas or hussar monkey ...	7
Genus *Cercocebus*, the mangabeys	
Cercocebus aethiops, sooty mangabey	5
Cercocebus torquatus, white-crowned mangabey	3
Genus *Macaca*, the macaques	
Macaca mulatta, the rhesus monkey	58
Genus *Papio*, the baboons	
Papio cynocephalus, yellow baboon	10
Papio hamadryas, hamadryas baboon... ...	1
Family CEBIDAE, the New World monkeys	
Genus *Cebus*	
Cebus azarae, Azara's capuchin	2
Genus *Lagothrix*, woolly monkeys	3
Genus *Ateles*, spider monkeys	
Ateles ater, black-face spider	5
Total	125

[1] The classification used by Zuckerman (1932) has been adopted (see Fulton and Zuckerman, 1934, in preparation).

III. *PONGO PYGMAEUS*, ORANG-UTAN

The arterial circle of Willis of the orang-utan is a polygon formed at the base of the brain by branches from the internal carotid and basilar arteries (fig. 1).

The internal carotid artery reaches the brain between the temporal lobe and the optic chiasm, runs antero-laterally a distance of 4 or 5 mm. and divides near the anterior perforated substance into its terminal branches, the anterior and middle cerebral arteries. It thus forms a part of the lateral boundary of the circle. The posterior communicating artery, much smaller in calibre than either of the other branches, forms a connection between the internal carotid and posterior cerebral arteries.

The middle cerebral artery, usually the larger of the two terminal branches of the internal carotid, runs laterally into the Sylvian fissure, taking no part in the formation of the arterial circle.

The anterior cerebral artery curves antero-medially, and is joined to its fellow of the opposite side by the anterior communicating artery to form an arch. From this arterial arch, separated from each other by 2–3 mm., two anterior cerebral arteries of approximately equal calibre run forward into the longitudinal fissure of the cerebrum. Within the fissure, each anterior cerebral artery lies on the medial surface of its respective hemisphere close to the rostrum and body of the corpus callosum. The artery sends cortical branches to the medial and superior aspects of the frontal and parietal lobes.

One merit of the nomenclature of the cortical branches of anterior cerebral artery given by Hindze (1927, 1930) for the gorilla and the chimpanzee is that the name of the vessel indicates its area of distribution. These branches were easily identified in most of the orang-utan brains which formed the basis of the present study. The following outline according to Hindze gives the distribution of the branches of the anterior cerebral artery:

1. Anterior perforating—to the anterior perforated substance.
2. Posterior orbital—to the rectus and the posterior part of the orbital gyri.
3. Anterior orbital—to the anterior part of the gyrus rectus and the orbital gyri, to the frontal pole, and the medial surface under the subrostral sulcus.
4. Anterior frontal—to the medial surface above the subrostral sulcus and the frontal pole.
5. Middle frontal—to the medial surface above the distribution of the anterior frontal artery and to the middle third of both frontal gyri.
6. Posterior frontal—to the medial and dorsal surfaces of the posterior third of the upper frontal gyrus.
7. Callosal—to the corpus callosum and its sulcus (as a distinct branch this was often absent on one or both sides in this series).
8. Superior precentral—to the paracentral lobule and the superior part of

the precentral and postcentral gyri. (Hindze does not mention its distribution to the precentral gyrus, but a relatively large twig is regularly present.)

9. Superior postcentral—to the same areas, a little posteriorly.

10. Precuneal—to the precuneus and the superior part of the postcentral gyrus.

The internal distribution of the arteries entering the anterior perforated space has been completely worked out by Beevor (1909) for the human, and since Shellshear (1927) has found their distribution in the orang-utan so similar to that of Man, the internal arteries have not been investigated in this study.

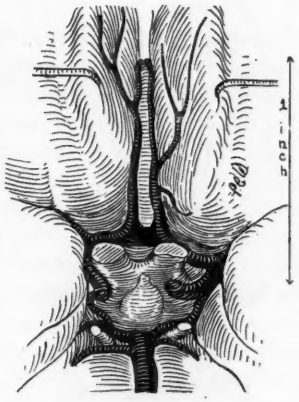

Fig. 1.

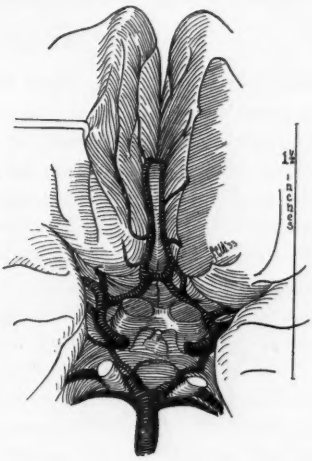

Fig. 2.

Fig. 1. Orang-utan. The two anterior cerebral arteries run parallel to each other and are joined together by a thick anterior communicating artery.

Fig. 2. Orang-utan. Like fig. 1. In addition, a loop is present in the left anterior cerebral artery, and a small branch joins the two posterior communicating arteries together.

The anterior communicating artery connects the two anterior cerebrals at the entrance to the longitudinal fissure. The communicating artery in the orang-utan is about 3 or 4 mm. long, and it has as great a diameter as the arteries which it connects.

The posterior cerebral arteries, formed by the bifurcation of the basilar at the upper border of the pons, make up the posterior boundary of the circle of Willis. The posterior cerebral passes anterior to the oculomotor nerve where the nerve leaves the brain, and then curves posteriorly around the cerebral peduncle.

In one specimen, the left anterior cerebral artery divides to form a loop close to the mouth of the longitudinal fissure (fig. 2). In the same brain, three distinct branches arise from the right internal carotid artery and are distributed to the territory of the middle cerebral artery; from the opposite carotid

arise two branches supplying this region of the left hemisphere. There is also a connecting branch between the posterior communicating arteries.

The fourth brain differs from those already described since it has three anterior cerebral arteries, the left with the usual branches and distribution (fig. 3). The right runs forward in the longitudinal fissure distributing branches to the gyrus rectus and the medial surface of the hemisphere below the corpus callosum. The anterior frontal artery, which is the terminal branch, runs near the cingulate sulcus to the superior frontal gyrus. The middle anterior cerebral artery runs forward into the fissure and lies close to the rostrum and body of the corpus callosum without branching until it reaches the middle third of

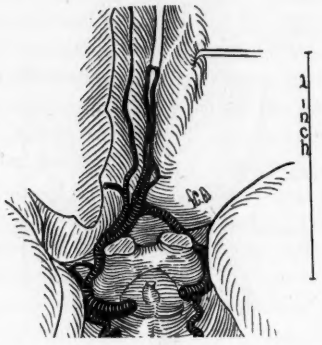

Fig. 3.

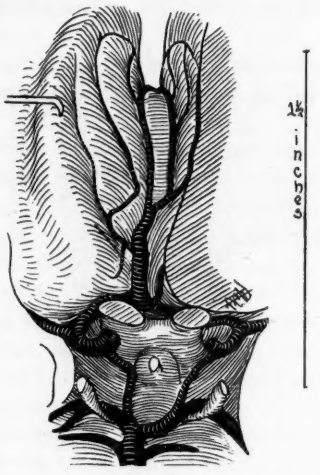

Fig. 4.

Fig. 3. Orang-utan. Three anterior cerebral arteries are present in this specimen.

Fig. 4. Chimpanzee. The large trunk formed by the union of the right and left anterior cerebral arteries bifurcates before reaching the genu of the corpus callosum. A rudimentary anterior cerebral arises just to the left of the main trunk.

the corpus callosum. Then the artery sends branches to the paracentral lobule and to the precuneous.

Three of the four orang-utans used in the present investigation have two anterior cerebral arteries which run parallel to each other within the longitudinal fissure, each lying on the medial surface of its respective hemisphere close to the corpus callosum. The arteries are jointed together at the entrance of the fissure by an anterior communicating artery of large size. The fourth brain has three anterior cerebral arteries which run within the fissure.

The reports of other authors relating to the cerebral blood vessels of the orang-utan are in general agreement with my findings. Tyson (1699) considered the arteries of the base of the brain in his specimen similar in every respect to those of Man. Bolk (1901) found the anterior communicating artery

absent so that the circle of Willis was not closed in the two orang-utan brains which he examined. Grünbaum and Sherrington (1902), like Tyson, noted that the circle of Willis in their specimen had an arrangement like that of a Man. Rothmann (1904) studied the brains of four orang-utans, in three of which there were two anterior cerebral arteries connected by a communicating branch, and in one there were three anterior cerebrals. In a recent study of the blood vessels of the brain, Shellshear (1927) observed two anterior cerebral arteries connected by a communicating branch; the left anterior cerebral divided to form a perforation just ventral to the medial olfactory stria.

IV. *PAN SATYRUS*, CHIMPANZEE

On superficial examination the circle of Willis and the anterior cerebral arteries of the chimpanzee appear very similar to those of the orang-utan. The posterior cerebral arteries are formed by the bifurcation of the basilar, and these are connected with the internal carotids by the smaller posterior communicating arteries. Likewise, the internal carotid artery divides into its two terminal branches, the middle and anterior cerebral. The middle cerebral artery runs laterally into the fissure of Sylvius without forming a part of the boundary of the polygon. A comparison of the relative size of the anterior and middle cerebral arteries of the six orang-utan brains, showed the middle was larger than the anterior in five of them. In the sixth brain, the anterior cerebral was larger than the middle on one side.

The anterior cerebral artery runs medially in a nearly transverse direction to unite with the same artery of the other side to form a single trunk which then passes into the longitudinal cerebral fissure (fig. 4). Within the fissure the artery continues as a single trunk nearly as far as the rostrum of the corpus callosum where it divides into two anterior cerebral arteries, one running along the medial aspect of each hemisphere supplying cortical branches on the way. Four of the specimens have a rudimentary left anterior cerebral artery which enters the longitudinal fissure (fig. 4). This gives the circle of Willis an appearance very similar to that of the orang-utan. However, this rudimentary vessel goes forward only to the frontal pole, and does not curve backward over the genu of the corpus callosum. Thus, the left anterior cerebral usually gives rise to the posterior orbital, the anterior orbital and the anterior frontal arteries to the left hemisphere. However, in fig. 4 the anterior orbital is seen to leave the left division of the main artery. Corresponding arteries to the opposite side originate from the unpaired trunk described above. Each terminal of the unpaired anterior cerebral artery sends a middle and posterior frontal, a superior precentral and postcentral, and a precuneal branch to its respective hemisphere. The precuneal artery can be followed into the parieto-occipital sulcus. In some cases a small twig continues along the sulcus of the corpus callosum and curves over the splenium.

Often there is no anterior communicating artery in the chimpanzee. When

a communicating artery is present, it is a short thick vessel between the rudimentary left anterior cerebral and the large anterior cerebral which sends branches to both hemispheres.

In one brain the anterior cerebral arteries run antero-medially, unite and enter the longitudinal fissure as a single trunk. This large trunk supplies branches to the gyrus rectus and the orbital parts of both frontal lobes (fig. 5). It bifurcates at the rostrum of the corpus callosum, one artery running on the medial surface of each hemisphere close to the body of the corpus callosum. A small branch continues posteriorly to the splenium.

The sixth specimen presents many abnormalities. A relatively large communicating branch lying under the posterior part of the optic chiasm connects the internal carotid arteries (fig. 6). From this vessel arises a branch which

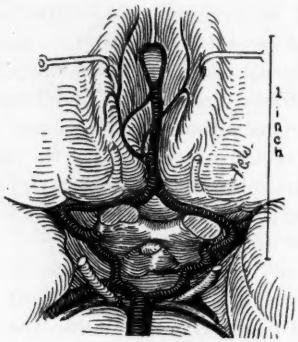

Fig. 5.

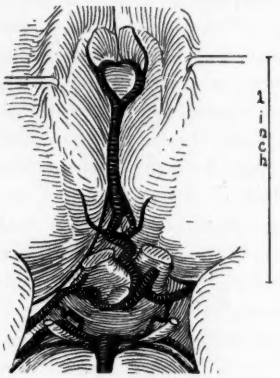

Fig. 6.

Fig. 5. Chimpanzee. Like fig. 4, but this specimen has no rudimentary anterior cerebral artery.
Fig. 6. Chimpanzee. An anomalous arrangement of the anterior cerebral arteries.

runs anteriorly under the chiasm between the two optic nerves and anastomoses with the anterior cerebral arteries. The right and left anterior cerebrals anastomose through a loop composed of a part of each and of the artery which passes between the optic nerves. From the loop a large single artery runs forward into the longitudinal fissure of the cerebrum. It bifurcates at the rostrum of the corpus callosum and follows the course already described in the other specimens. It may be seen that a relatively large branch from the right internal carotid lies on the inferior surface of the right optic nerve. A prominent branch springs from each side of the loop, and corresponds roughly to the posterior orbital artery.

In all six chimpanzees which have been described the two anterior cerebral arteries unite at the entrance of the longitudinal fissure of the cerebrum. This unpaired artery runs forward in the fissure to the rostrum of the corpus callosum where it divides into two anterior cerebral arteries, one passing along

the medial aspect of each hemisphere close to the corpus callosum supplying cortical branches on its way. In four of the specimens a second anterior cerebral artery arises from the arterial arch to the left of the main trunk, runs forward in the great fissure and distributes itself as far as the frontal pole. The circle of Willis in the brains just mentioned resembles that in Man. The fifth brain shows an arterial circle which is similar to that of the Cercopithecidae. In the sixth an anomalous artery arising from the internal carotid arteries joins the two anterior cerebrals. From the site of the anastomosis of the three arteries arises a single vessel which has the usual distribution within the longitudinal fissure.

There are no essential differences between the observations made upon the present specimens and the earlier descriptions of the circle of Willis in the chimpanzee which have been found in the literature. Sperino (1897) found the superficial cerebral circulation of the chimpanzee similar to that of a normal man. Grünbaum and Sherrington (1902) noted that the arterial circle resembled that of Man in four specimens; in a fifth there was a lateral fusion of the two anterior cerebral arteries at the usual site of the anterior communicating artery. Rothmann (1904) examined one chimpanzee brain in which the circle of Willis was like that of Man, another which had two anterior cerebral arteries but lacked the communicating branch, and five brains which had the type of circle seen in the Cercopithecidae. Only Shellshear (1930) and Hindze (1930) have described the distribution of the anterior cerebral artery of the chimpanzee after it leaves the circle of Willis. Shellshear found that the anterior cerebral artery passed antero-medially to the commencement of the longitudinal fissure where it joined its fellow to form a single trunk. The unpaired artery extended to the genu of the corpus callosum and divided into two anterior cerebral arteries. Hindze's specimen presented a large right anterior cerebral artery which supplied parts of both hemispheres with branches, and, in addition, had a rudimentary left anterior cerebral which was distributed to the medial surface of the left hemisphere below the corpus callosum.

V. HYLOBATIDAE, THE LESSER APES

Since the arteries of the two available gibbon brains were so similar to the Cercopithecidae a detailed description will not be undertaken. As in the Cercopithecidae, the posterior cerebral arteries are formed by the bifurcation of the basilar and they are joined to the internal carotid arteries by the posterior communicating (fig. 7). Likewise, the internal carotid artery divides into two terminal branches, the middle and anterior cerebral arteries. The anterior cerebral artery runs antero-medially, joining its fellow of the opposite side to form a single trunk which enters the longitudinal fissure of the cerebrum. Within the fissure the unpaired artery passes forward lying close to the rostrum and body of the corpus callosum. From one brain a block of tissue had been removed which made it impossible to follow the artery through its entire

length. In the other the artery continues posteriorly from the genu giving cortical branches to both hemispheres. Bifurcation of the main trunk occurs in the posterior third of the corpus callosum, where each terminal artery divides into several branches distributed to the medial aspect of the parietal lobe. A small vessel continues the course of the main artery along the corpus callosum to the splenium. In both brains the right anterior cerebral artery is better developed than the left, being twice or three times as large.

The arteries of only a few gibbon brains have been described. Waldeyer (1891) stated that the arteries of the base of the gibbon brain are essentially like those of Man. According to Bertha de Vriese (1905), Sperino (1898) found that the circle of Willis of the gibbon corresponded in all particulars with that of Man. However, Rothmann (1904) noted that the two anterior cerebral

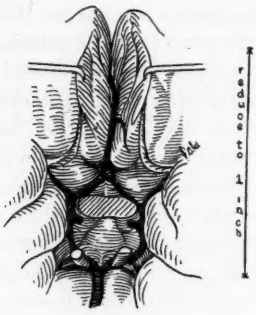

Fig. 7.

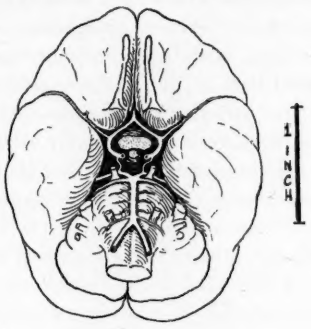

Fig. 8.

Fig. 7. Gibbon. The two anterior cerebral arteries unite to form a single trunk as in the Cercopithicidae.

Fig. 8. *Macaca mulatta.* The two anterior cerebral arteries unite at the entrance of the longitudinal fissure.

arteries united to form a single trunk in three brains. In a fourth specimen, instead of a single trunk, two arteries arose from the point of union of the anterior cerebral arteries, one running antero-laterally to the right and the other antero-laterally to the left. The anterior cerebral artery and the circle of Willis in both of the gibbon brains examined here belonged to the type found in the Cercopithecidae.

VI. CERCOPITHECIDAE, THE OLD WORLD MONKEYS

The brain of the Cercopithecidae receives the usual blood supply from the internal carotid and basilar arteries. Branches of the two anastomose to form a polygonal circle of Willis.

The internal carotid artery reaches the brain between the tuber cinereum and the temporal lobe, curves forward 3 or 4 mm. and divides into its terminal branches, the anterior and middle cerebral arteries. The internal carotids are

usually equal in size and symmetrical on both sides. A small posterior communicating artery connects the internal carotid with the posterior cerebral artery (fig. 8).

The middle cerebral artery runs antero-laterally into the fissure of Sylvius and forms no part of the polygon. Its calibre is equal to that of the anterior cerebral in 40 per cent. of the specimens, is larger in 33 per cent. and smaller in 27 per cent.

The anterior cerebral artery runs antero-medially toward the longitudinal fissure of the cerebrum where it unites with its fellow of the opposite side to form a single vessel which passes forward into the fissure (fig. 8). There is no anterior communicating artery. Within the longitudinal fissure, the unpaired anterior cerebral artery lies close to the rostrum and the body of the corpus callosum, sometimes more in contact with the medial surface of one hemisphere and then with the other. It sends cortical branches to the medial and superior surfaces of the frontal and parietal lobes of both hemispheres. There are an equal number of specimens in which the artery divides in the middle third of the corpus callosum and in which the division occurs in the posterior third. In only 12 per cent. did a small branch continue on to the splenium after the main artery bifurcated.

The corresponding branches to the two hemispheres leave the anterior cerebral artery close together but not always opposite each other. Not infrequently there are one or two more branches to one hemisphere than to the other. The nomenclature adopted for the cortical branches of the anterior cerebral artery of the Cercopithecidae is a slight modification of that used for the orang-utan and chimpanzee. The distribution is as follows:

1. Posterior orbital—to the gyrus rectus and posterior part of the orbital gyri.

2. Anterior orbital—to the anterior part of the gyrus rectus, the frontal pole, and the medial surface under the rostral sulcus.

3. Anterior frontal—to the medial surface above the rostral sulcus and to the frontal pole.

4. Middle frontal—to the medial surface above the anterior frontal artery, to the middle part of cingulate and marginal gyri, and to the superior frontal gyrus.

5. Posterior frontal—to the medial surface above the middle frontal artery, to the cingulate and marginal gyri, and the superior part of the premotor area.

6. Parietal—to the posterior portion of the marginal gyrus and the superior part of the precentral and postcentral gyri. In some specimens there is one vessel leaving the main artery and in others there are two branches distributed to this region.

7. Precuneal—to the precuneous and the superior part of the postcentral gyrus, often to the interparietal and parieto-occipital sulci.

In 12 per cent. of the specimens examined a tiny twig continues along the corpus callosum to the splenium after the main artery bifurcates.

The posterior cerebral arteries produced by the bifurcation of the basilar run laterally a short distance and curve posteriorly around the cerebral peduncles. Through the first part of its course the artery is parallel to the superior cerebellar artery from which it is separated by the oculomotor nerve.

A number of variations of the anterior cerebral artery are worthy of note.

In five *Macaca mulatta* and one *Papio cynocephalus* the arteries, after uniting, redivide to produce a loop (fig. 9). In three specimens the loop is 2–3 mm. long and in two only 1 mm. In one of the specimens the lumina of the vessels have no connection in the proximal part of the loop.

In four *Macaca mulatta* and one *Cercocebus aethiops* the anterior cerebral arteries entered the longitudinal fissure as separate vessels and united 3–4 mm. within the fissure (fig. 10).

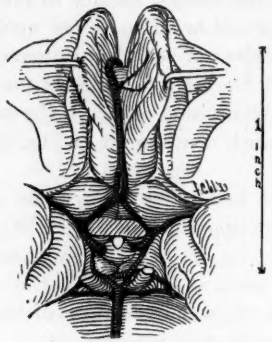

Fig. 9.

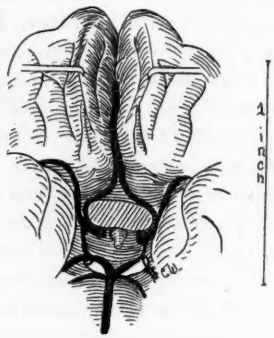

Fig. 10.

Fig. 9. *Macaca mulatta.* After union of the anterior cerebral arteries, the main trunk divides to form a loop.

Fig. 10. *Macaca mulatta.* The right and left anterior cerebral arteries enter the longitudinal fissure separately, and unite several millimetres within it.

One *Macaca mulatta* presented a picture like the preceding except that the two arteries were united at the mouth of the fissure by a communicating branch (fig. 11). This gave the circle of Willis a form closely resembling that of Man.

Two specimens, a *Macaca mulatta* and a *Cercocebus aethiops*, show a relatively large branch leaving one anterior cerebral artery before it joins its fellow. This branch supplies the posterior part of the orbital gyri, thus taking over some of the function of the first branch of the unpaired trunk. A drawing of one specimen of *Ateles ater* shows this quite clearly (fig. 12).

A *Papio cynocephalus* has a similar branch originating from the left anterior cerebral artery which runs forward into the longitudinal fissure a distance of 10 mm., crosses the mid-line passing over the common trunk and sends twigs to the medial surface and the gyrus rectus of the opposite side.

In a *Cercocebus aethiops* the right anterior cerebral is unusually large and

the left very small so that, although the two unite into one trunk, nearly all of the blood to the medial surfaces of the frontal and parietal lobes of both hemispheres was supplied through one internal carotid artery. A *Cercopithecus sabeus* presents a similar variation, except that the left artery is much the larger.

The Cercopithecidae present a definite type of arterial circle. The anterior cerebral arteries run antero-medially, unite, and enter the longitudinal fissure of the cerebrum. Within the fissure this unpaired artery gives rise to branches distributed to the medial and superior surfaces of the frontal and parietal lobes of both hemispheres. Of the 103 specimens studied seventeen vary a little from the usual form. The variations are shown in figs. 9, 10, 11 and 12.

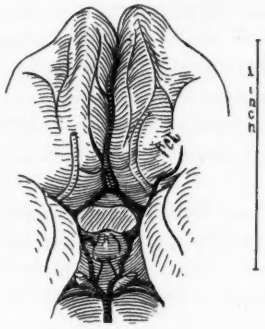

Fig. 11.

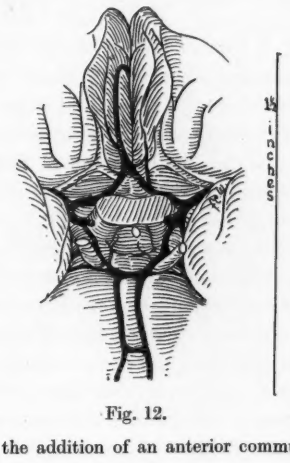

Fig. 12.

Fig. 11. *Macaca mulatta.* Similar to fig. 10, with the addition of an anterior communicating artery.

Fig. 12. *Ateles ater.* The rudimentary anterior cerebral artery to the left of the main trunk is like that of the chimpanzee. A double basilar artery joined together by transverse branches is characteristic of *Ateles ater.*

In no specimen did the two arteries extend more than a few millimetres into the fissure before uniting, and in no instance did this unpaired artery bifurcate before reaching the middle third of the corpus callosum.

As quoted in the Introduction, Theile (1852) in three *Simia inuus* found that the two anterior cerebral arteries united to form a single trunk which gave rise to branches to both hemispheres.

Other authors, among whom are Stannius (1850), Staderini (1889), Rojecki (1889), and Lesem (1905), observed that the two anterior cerebral arteries united into a single trunk near the entrance of the longitudinal fissure in various species of Cercopithecidae.

Rothmann's (1904) investigation of the anterior cerebral artery included thirty-two "niedere Affen." The two anterior cerebral arteries united into a

single trunk in twenty of the brains. Five other specimens showed a single loop in the unpaired artery, and one a double loop. In two brains, one anterior cerebral artery was much larger than its fellow, and in another brain one anterior cerebral was absent so that the medial surfaces of both hemispheres were supplied with blood through a single internal carotid. Three brains showed a branch leaving the first part of one anterior cerebral artery making the circle of Willis resemble the circle of the chimpanzee with its main and rudimentary anterior cerebrals.

Critchley's (1930) description of the distribution of the anterior cerebral artery in the baboon conforms in general to that given here.

VII. CEBIDAE, THE NEW WORLD MONKEYS

Only a few specimens of the Cebidae were available for examination, but from the material at hand it would appear that there are no marked differences between the genus *Cebus* and genus *Lagothrix* and the Cercopithecidae. The anterior cerebral arteries unite to form a single trunk which, within the longitudinal fissure, has branches of distribution to both hemispheres. The circle of Willis presents the usual form and the calibre of the arteries bear the same relationship one with the other.

The anterior cerebral arteries unite several millimetres within the longitudinal fissure in one *Lagothrix* (as in fig. 10). In another *Lagothrix* the two anterior cerebral arteries are joined together by a short communicating branch at the entrance of the longitudinal fissure, and 5 mm. within the fissure the anterior cerebrals unite into a single trunk (as in fig. 11). Both of these forms are seen in the Cercopithecidae and considered variations, but here one cannot say which is usual and which unusual.

Certain distinct differences are present in the *Ateles ater* which were not seen in other species of the Cebidae nor in the Cercopithecidae. A slightly different method of presentation will be used in order to emphasise their significance.

After reaching the intracranial cavity between the optic chiasm and temporal lobe, the internal carotid artery divides into two branches, an anterior and a posterior. The posterior branch runs caudally, approaching its fellow of the opposite side as it nears the pons. In its course the artery gives origin to a collateral branch which passes anterior to the oculomotor nerve and curves around the cerebral peduncle. This branch is the posterior cerebral. The posterior branch of the internal carotid, the posterior communicating artery, continues caudally as the basilar, which is double (fig. 12). The basilar arteries are parallel from the upper to the lower margin of the pons where they diverge and continue as the vertebrals. In their parallel course, the basilars are joined together by a transverse anastomosing branch near each end. One specimen, instead of anastomosis by transverse arteries, shows a lateral fusion of the basilars for a distance of 2 mm. at the lower and 4 mm.

at the upper level of the pons. In another specimen there is a fusion for 5 mm. at the upper border of the pons, but none at the lower border.

The anterior division of the internal carotid artery runs antero-medially to unite with its fellow. This unpaired anterior cerebral artery enters the longitudinal fissure, and has a distribution as shown in fig. 9. Before its union with the opposite anterior cerebral artery, it gives origin to the middle cerebral artery which passes laterally into the fissure of Sylvius.

There is considerable individual variation of the anterior cerebral arteries in the *Ateles ater* which will be briefly noted. In the first specimen they united 3–4 mm. within the longitudinal fissure. In the second there is a small loop in the first part of the left anterior cerebral, from which two twigs pass diagonally to the posterior orbital region. In the third specimen there are two anterior cerebral arteries given off from each internal carotid (fig. 13). The larger anterior cerebral arteries unite in the usual way at the lips of the fissure; the smaller arteries curve laterally around the larger and join the unpaired anterior cerebral artery 2 mm. anterior to its source. The arteries of the fourth brain have a resemblance to the circle of Willis of the chimpanzee. In addition to the typical unpaired artery within the fissure, a branch from the first part of the left anterior cerebral runs forward over the gyrus rectus almost to the frontal pole (see fig. 12).

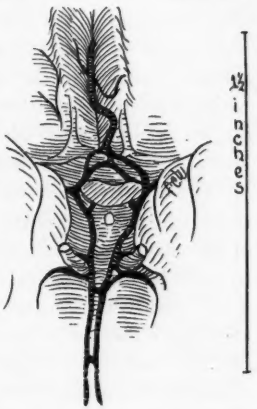

Fig. 13. *Ateles ater*. The double basilar is like that in fig. 12. Two anterior cerebral arteries from the right unite with their fellows of the left near the entrance of the longitudinal cerebral fissure.

Elze (1910) has drawn attention to the double basilar artery in the *Ateles ater* and presents excellent diagrams indicating the type of anastomosis between the arteries. In half of his specimens the basilar arteries were joined together at different levels by transverse branches of various thicknesses. In the fourth there was a short lateral fusion of the arteries at the anterior third of the pons. The fifth specimen was similar to the fourth except that it was complicated by the presence of a loop at the level of the lateral fusion. The sixth had a single basilar artery which divided to form a loop, but otherwise did not differ greatly from the basilar of other species.

Although an occasional loop was found, a double basilar artery was not present in a single specimen of the entire series of 125, except *Ateles ater*.

VIII. COMPARISONS AND CONCLUSIONS

For purposes of comparison with the other Primates it may be permissible to say here, that in Man the anterior cerebral artery arises from the internal carotid, runs antero-medially and enters the longitudinal fissure. Within the fissure it lies on the medial surface of the hemisphere close to the rostrum and body of the

corpus callosum and sends cortical branches to the frontal and parietal lobes. At the entrance of the fissure the anterior cerebral arteries are connected by a short anterior communicating artery. It is evident from the descriptions and diagrams presented by Rothmann (1904) in two cases, and by Hindze (1927, 1930) in two, that the circle of Willis and the anterior cerebral artery of the gorilla are more nearly like those of Man than any other Primate.

Next to the gorilla, the arteries of the orang-utan resemble those of Man most closely. There are two anterior cerebral arteries in all of the orang-utans in this series and in all described in the literature, except one observed by Rothmann (1904) and one cited here, both of which had three arteries. An anterior communicating artery connects the anterior cerebrals at the entrance of the longitudinal fissure in all except the two specimens observed by Bolk (1901) in which the communicating branch was absent. The anterior communicating artery of the orang-utan differs strikingly from that in Man in this series and in the specimens studied by Rothmann (1904). The artery has a diameter as great as that of the vessels it unites. The two anterior cerebral arteries united by the communicating branch form an arterial arch from which the anterior cerebral arteries which enter the fissure arise at right angles. Each artery supplies the medial surface of the frontal and parietal lobes of its respective hemisphere with blood.

The anterior cerebral arteries of the chimpanzee unite at the entrance of the longitudinal cerebral fissure, run forward as a single trunk to the rostrum of the corpus callosum where the trunk redivides into two branches, one going to each hemisphere. In some specimens there is a rudimentary artery arising a few millimetres to the left of the common trunk, which passes forward into the fissure and gives branches to the medial surface as far as the frontal pole, but not above the corpus callosum. The same distribution of the arteries was found by Shellshear (1930) and by Hindze (1930), and the appearance of the circle of Willis in five of Rothmann's chimpanzees indicates that union of the two anterior cerebral arteries occurs frequently. There were two anterior cerebral arteries connected by a communicating branch in four specimens examined by Grünbaum and Sherrington (1902). These authors made no observations on the course of the arteries within the longitudinal fissure.

It would appear that the anterior cerebral artery and the circle of Willis of the gibbon resemble the human type in some specimens and the Cercopithecidae type in others. Sperino (1898) and Waldeyer (1891) found the arrangement of the arteries was similar to that of Man; in this series and in Rothmann's (1904) the type was found to be similar to that seen in the Cercopithecidae.

A sufficiently large number of Cercopithecidae have been examined to say that in this family the anterior cerebral artery runs antero-medially toward the longitudinal fissure of the cerebrum where it unites with its fellow of the opposite side to form a single vessel which passes forward into the fissure. There is no anterior communicating artery. Within the fissure, this unpaired

artery lies close to the rostrum and body of the corpus callosum, and sends cortical branches to the medial and superior surfaces of the frontal and parietal lobes. Certain variations in the course of the anterior cerebral artery have been observed. The contributions of Stannius (1850), Theile (1852), Staderini (1889), Rojecki (1889), Rothmann (1904), Lesem (1905), and Critchley (1930) confirm the observations on the anterior cerebral artery and circle of Willis which were made in the present study.

The genus *Cebus* and genus *Lagothrix* of family Cebidae conform to the type established for the Cercopithecidae. Likewise, except for marked individual variations, the anterior cerebral artery of the specimens of *Ateles ater* belong to this type.

However, a most striking characteristic differentiates the *Ateles ater* from the other species examined, that is, the presence of a double basilar artery. The double basilar was present in all individuals of this species but was not present in a single specimen in the entire remaining 125 Primate brains. Elze (1910) has previously called attention to the double basilar artery in the *Ateles ater*.

The family differences as well as the individual variations become more easily understandable in light of the excellent work of Bertha de Vriese (1905). She made a careful study of the literature relating to the cerebral arteries of many lower animals, and herself examined a series of human embryos and the embryos of lower animals. She found that the internal carotid artery is more primitive than the vertebral, and that the carotid supplies the entire brain in the early stages of embryonic life. It divides into a large cranial and a large caudal branch. The anterior cerebral artery is a continuation of the cranial branch and the middle cerebral is a collateral. In the early stages of embryonic life the anterior cerebral arteries run parallel to each other without a connection between them. They become united by a communicating network from which arises a median artery which can become the unpaired anterior cerebral artery. In animals having a single artery the lateral arteries atrophy. In species which have parallel anterior cerebral arteries it is probable that the median artery atrophies.

Bertha de Vriese (1905) also determined that primitively the basilar artery is the termination of the caudal branch of the internal carotid, and in the early stages the basilar is double. Transverse anastomosing vessels develop and later loops are found along the course of the two basilar arteries; and finally, through further development in some places and atrophy in others, an unpaired basilar artery results. The posterior cerebral artery is a collateral of the caudal branch of the internal carotid, and the small posterior communicating artery is all that remains of the caudal branch.

I am deeply indebted to Dr John F. Fulton for placing his valuable material at my disposal and for his many criticisms and suggestions. I also wish to thank Mrs Frances C. Woodhall and Mr Armin Hemburger for the interest and care they have taken in the execution of the drawings.

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ABSENCE OF THE RIGHT COMMON CAROTID ARTERY

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Obliteration of the ductus caroticus of the original branchial arch pattern, that is, the portion of the embryonic dorsal aorta between the third and fourth arch vessels, is a very constant feature of mammalian development, and, as naturally follows, the absence of the common carotid artery, an abnormality which entails the persistence of the ductus caroticus and the disappearance of the third arch vessel, is extremely rare. Malacarne (1), in 1784, seems to have been the first to describe the condition. In his example of it a double aortic arch was present and on each side the external and internal carotid arteries had separate origins from the aortic arch. Since Malacarne's description of the absence of the common carotid artery there have been, to my knowledge, only six recorded cases of the abnormality. Power (cited by Richard Quain (2)) dissected a subject in which the right common carotid stem was absent; Kosinski (3) described the separate origin from the innominate artery of the two carotid arteries of the right side. Gottschau (4) described a case in which the left carotid vessels arose separately from the arch of the aorta, no left common carotid artery being present. Macalister (5) described the absence of the right common carotid artery, and von Angemeyer (6) a similar condition on the left side. Poynter (7), in 1916, reviewed the literature of this condition, but he had no case of his own to record. Fife (8), in 1921, described a case in which a right aortic arch was present and from which the internal and external carotid arteries arose separately; the left subclavian artery, in this subject, arose from the dorsal aorta.

Bifurcation of the common carotid artery at a low level, with consequent shortness of the vessel, has been recorded by Morgagni (9), Kantor (10), Orr (11) and Adachi (12).

DESCRIPTION OF CASE

Dissecting room subject, female, age 53. Cause of death was carcinoma of the stomach.

An examination of the region of the common carotid artery in the routine dissection of the right side of the neck revealed two arteries passing upwards in a common, but loose, carotid sheath. The internal jugular vein lay posterolateral to the more posterior of the two arteries, and the vagus nerve was found between this artery and the vein. Careful dissection downwards showed that the anterior artery arose as the cephalic branch of the innominate bifurca-

tion and that the posterior artery arose from the right subclavian artery about half an inch (10 mm.) beyond the bifurcation (see fig. 1).

The anterior vessel, when traced upwards, gave off branches which arose and were distributed as are those of a normal external carotid artery. The superior thyroid artery was the first branch and it arose from the external carotid artery at the level of the upper border of the thyroid cartilage. The posterior vessel, or internal carotid artery, passed upwards without giving off any branches. Its course was parallel to the external carotid artery, and it maintained a distance of about half an inch from that vessel throughout its passage. Above the level of the thyroid cartilage its course was similar to that of a normal internal carotid artery, except that it had a slight tortuosity with the concavity directed forwards. This tortuosity included the whole length of the internal carotid artery above the level of the posterior belly of the digastric muscle. The internal carotid artery terminated its cervical course by entering a normally situated carotid canal.

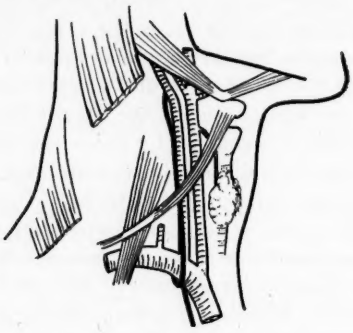

Fig. 1.

The relations of the two arteries in the lower part of the neck were similar to the normal relations of the common carotid artery. The right vagus nerve passed down inside the vascular sheath between the internal jugular vein and the internal carotid artery; in the lower part of its course it passed to the lateral surface of the internal carotid artery. It crossed superficial to the subclavian artery and passed in the usual manner into the thorax. A recurrent branch was given off and this nerve passed deep to the subclavian artery and then upwards and medialwards below the carotid vessels to reach its normal position. The right ansa subclavia was found looping around the subclavian artery distal to the origin of the internal carotid branch. The internal mammary artery and the thyro-cervical axis arose from the first part of the subclavian artery beyond the origin of the internal carotid artery, and these vessels were normal in their distribution except that the right suprascapular artery arose from the third part of the subclavian artery. The right vertebral artery was normal in origin and position, but it entered the foramen in the transverse process of the fourth cervical vertebra.

Fortunately, in the preparation of this body for dissection, the injection had been introduced through the external carotid artery, and, hence, it was possible to examine the calibre and to study the intimate relations of the internal carotid artery in detail. An examination of the glosso-pharyngeal nerve was first made to determine if a carotid branch (the *sinus nerve* of Hering) could be found. The deep dissection of the upper part of the neck had not been commenced, so that there had been no interference with the nerve by the student dissectors. The glosso-pharyngeal nerve was carefully isolated and its branches dissected, but I could find no trace of a nerve which could be considered to be the sinus nerve[1].

The internal carotid artery, the undamaged portion of the external carotid artery, and the space between them were then carefully dissected to determine if the carotid body was present. This dissection was carried out while the vessels were still undisturbed and lying in their sheath, the only interference having been the incision into the lower part of the external carotid artery which had been ligatured above and below the incision. No structure was found which could be taken to be the carotid body.

When these examinations were completed, the innominate artery and the subclavian artery, the latter well beyond the origin of the internal carotid artery, were divided and the specimen was removed after dividing the internal carotid artery and the branches of the external carotid artery high up in the neck. The external measurements of the vessels at different points were then recorded (see Table I).

Table I. *External calibre of vessels in mm.*

	Below innominate bifurcation		Beyond origin of vessels											
	1 cm.	2 cm.	Immediately beyond	1 cm.	2 cm.	3 cm.	4 cm.	5 cm.	6 cm.	7 cm.	8 cm.	9 cm.	10 cm.	11 cm.	12 cm.
Innominate artery	16	17	—	—	—	—	—	—	—	—	—	—	—	—	—
Subclavian artery	—	—	11	10	10	—	—	—	—	—	—	—	—	—	—
Internal carotid artery	—	—	7	7	6·5	6·5	6	6	6	6	6	6	6	6	6
External carotid artery	—	—	8	7	7	6	6	6	6	6	6	—	—	—	—

It will be seen from these measurements that there was no dilatation on the course of the internal carotid artery and, therefore, it would seem that

[1] I have, during the past two years, collected notes on the carotid branch of the glosso-pharyngeal nerve in all those dissecting room bodies in which there had not been previous interference with the region by the students of the practical anatomy class. The nerve has been found in the examination of a series of fifty-eight glosso-pharyngeal nerves, and the present case is the only one in which I was unable to find the carotid branch. This fact leads me to believe that if the sinus nerve had been present in the subject under discussion, it would have been found.

no carotid sinus (*bulbus caroticus*) is present on the right side of this subject[1]. The wall of the vessel was examined for any local area of thinning, but no trace of the thinning, which is characteristic of the carotid sinus, could be found. An attempt was made to study the wall of the carotid artery histologically, but the preservation of the tissues was not sufficiently good to justify me in arriving at any conclusions concerning the presence or absence of those microscopic features which are characteristic of the intimate structure of the carotid sinus.

The heart, in this subject, was normal; and no other modifications of the aorta, or of its branches, were present. The left common carotid artery was present and it bifurcated at its normal level. There was a definite dilatation of the commencement of the left internal carotid artery, and a carotid branch of the left glosso-pharyngeal nerve was found. The left carotid body was found in the angle of the bifurcation of the common carotid artery. The hepatic artery in this body was a branch of the superior mesenteric artery.

DISCUSSION

The explanation of the abnormality which has been described is not difficult in terms of the classical conception of branchial arch differentiation (see fig. 2). The ductus caroticus would appear to have remained patent on the right side and the third right aortic arch vessel to have disappeared (fig. 2 D). The mechanical factors involved in the production of this abnormality are not easily understood. There do not appear to have been any abnormal mechanical influences originating outside the vessels which could have had a moulding effect on the final result. The normal position of the heart and aorta precludes an explanation of the production of the abnormality by an abnormal blood current. It would be interesting to know if the disappearance of the third arch vessel was the primary condition, with persistence of the ductus caroticus as a result. This appears to me, by analogy, to be more likely than a primary persistence of the ductus caroticus as the determining factor in the production of the abnormality.

The work of Congdon (13) on the changes undergone by the branchial arch vessels in the human subject during embryonic development has shown that these changes have not the simplicity which is suggested by the usual text-book diagrams. He has shown that paired ventral aortae do not appear during human development, the aortic arches arising from a common ventral sac, the aortic sac. The third aortic arches are retained, in the subsequent stages of development, as the roots of the internal carotid arteries, and the external carotid arteries arise later from the anterior aspects of these third arch vessels (see fig. 3 A). At a later stage the aortic sac bifurcates cranially and splits into systemic and pulmonary trunks. The left cranial limb of the sac is then

[1] The slight conical dilatation at the commencement of the internal carotid artery I take to be the *Ursprungskegel* of Roux. It is to be found on the commencement of normal common carotid arteries.

continued more directly into the left fourth arch vessel and forms the base of the systemic aorta. Associated with these changes is the migration upwards of the origins of the subclavian arteries along the right and left dorsal aortae.

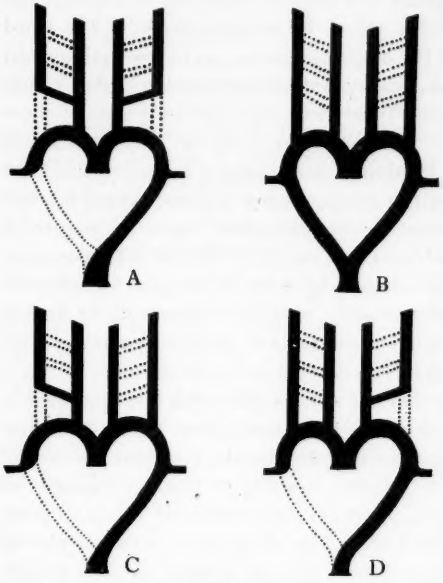

Fig. 2.

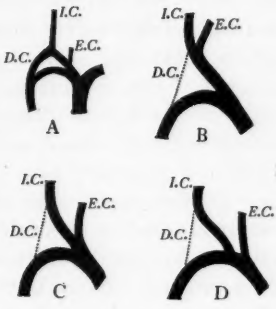

Fig. 3.

Fig. 2. Diagrams of the first four branchial arch arteries to show how absence of the common carotid arteries can be explained in terms of branchial artery development. A, normal pattern. B, Malacarne's case in which both aortic arches have persisted and the carotid arteries of each side take separate origins from the arch. C, normal development of the aortic arch but separate origins of the left carotid vessels from the arch (Gottschau, v. Angemeyer). D, normal development of the aortic arch but separate origins of the right carotid arteries from the right fourth arch artery (Kosinski, and in the subject described in the present paper).

Fig. 3. Diagrams to show an alternative explanation of absence of the common carotid artery. A (modified from Congdon), the normal early pattern of the right branchial arteries before the ductus caroticus has disappeared; the third and fourth arch vessels are arising from the right limb of the aortic sac and are joined posteriorly to the right dorsal aorta; the separate origin of the external carotid artery from the third arch vessel is shown. B, the carotid system in which a normal common carotid artery is present. C, a very short common carotid artery owing to more caudal attachment of the external carotid artery to the third arch vessel. D, the absence of the common carotid artery when the external carotid artery takes its origin from the right limb of the aortic sac. *E.C.* external carotid artery; *I.C.* internal carotid artery; *D.C.* ductus caroticus.

At or about the 14 mm. stage the right dorsal aorta disappears between the origin of the subclavian artery and the point at which it is joined by the right third arch vessel, so that the fourth arch vessel becomes the commencement

of the right subclavian artery; meanwhile the right limb of the aortic sac has elongated to form the innominate artery from which the right common carotid and subclavian arteries take their definitive origins.

It will be seen that this description still permits of an explanation of the absence of the right common carotid artery by disappearance of the third right arch vessel and persistence of the ductus caroticus, as has been described above. An alternative explanation, however, also suggests itself, and it has the added merit of readily explaining those cases in which only a very short common carotid artery is present. It seems to me that the external carotid artery might take origin from the third arch vessel nearer the aortic sac than is usual; in this circumstance either the common carotid artery would be very short (see fig. 3 C) or, if the origin were far enough caudal, the common carotid artery would be absent and the internal and external carotid arteries would then arise separately from the aortic sac (see fig. 3 D). If this can be accepted as a possible explanation of the abnormality, then persistence of the ductus caroticus is not an invariable factor in the production of the vascular developmental abnormality in which the common carotid artery is absent.

I am more inclined to the view that the abnormality which is described in this paper was due to disappearance of the third arch vessel with persistence of the ductus caroticus. My opinion is supported by the fact that no carotid sinus was present on the abnormal vessels. A study of the development of the carotid body and of the carotid sinus (14) has convinced me that these structures are derivatives of the third arch. The sinus nerve, which is closely concerned in the normal development of the third arch vessels, was also absent. The absence, in this subject, of these third arch derivatives suggests that the third right branchial arch vessel is not represented in the persisting vessels; it disappeared early in development or, possibly, was never present.

SUMMARY

1. A rare abnormality of the vascular system, absence of the right common carotid artery, is described.

2. It is suggested that this condition is due either to disappearance of the third right branchial arch vessel with persistence of the ductus caroticus, or to the secondary origin of the external carotid artery being more caudal than is usual. The present case is regarded as due to the former cause.

3. Absence of the carotid sinus and of the sinus nerve on the side of the abnormality is described.

I am indebted to Prof. Walmsley for his helpful criticism and to Miss M. E. Rea, B.A., for the figures.

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LE NEOPALLIUM DU BŒUF. ÉTUDE DE SON DÉVELOPPEMENT ET INTERPRÉTATION DE SES PLISSEMENTS

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CE travail fait suite à nos publications antérieures sur le neopallium des Équidés[1] et sur le neopallium des Suidés[2]. L'ensemble de toutes ces recherches aboutira, nous l'espérons, à une synthèse morphologique du cerveau des Ongulés.

De même que dans nos publications précédentes, nous donnons, parallèlement à notre étude du développement du neopallium, et à titre complémentaire, quelques indications sur celui du rhinencéphale.

En nous basant sur l'état du développement des très nombreux cerveaux que nous avons eu à notre disposition et qui proviennent des abattoirs de Varsovie, nous avons pu établir 10 stades, dont les 8 premiers se rapportent à l'état fœtal. Le stade IX correspond à un moment proche de la naissance; le stade X est le stade adulte.

Pour l'établissement de ces stades, la taille de l'animal n'a pas été prise en considération, car, ici, comme ailleurs, elle est loin de correspondre toujours à l'état du développement du cerveau[3].

	Nos.[4]	Longueur du télencéphale en mm.	Hauteur du télencéphale en mm.
Stade I	68	13	11
„ II	67	20	15
„ III	52	19	14
„ IV	1	29	20
„ V	33	33	23
„ VI	23	39	24
„ VII	15	42	26
„ VIII	3	45	29
„ IX	18	50	33
„ X (adulte)	—	117	67

[1] R. Anthony et J. de Grzybowski: "Le neopallium des Équidés. Étude du développement de ses plissements," *J. Anat.* vol. LXIV, Jan. 1930.

[2] R. Anthony et J. de Grzybowski: "Le neopallium des Suidés. Étude de son développement et interprétation de ses plissements," *Arch. de Zool. expér. et gén.* Volume jubilaire, t. LXXIV, 1931.

[3] Voir R. Anthony et J. de Grzybowski, publications citées ci-dessus.

[4] Ces numéros correspondent à l'inscription de ceux de nos matériaux qui ont été utilisés au cours de la rédaction de ce travail; ces matériaux ont été ainsi cotés au fur et à mesure que nous nous les procurions.

STADE I

A ce premier stade, le cerveau du bœuf se range, en ce qui concerne la forme extérieure, entre celui du cheval et celui des Suidés.

Indice: $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}} = 84{\cdot}6$. Cet indice est de 88·8 chez le porc et de 82·8 chez le cheval. Le cerveau du bœuf tend ainsi, plus que celui du cheval et moins que celui du porc, à se rapprocher de la forme sphérique. La forme subsphérique serait donc un caractère du cerveau des Ongulés au début de son développement; son allongement constant chez l'adulte ne se produirait qu'ultérieurement.

Le bord postérieur du cerveau est presque aussi oblique de haut en bas et d'arrière en avant que chez l'ours blanc à un stade comparable, c'est-à-dire à la naissance[1].

La surface télencéphalique est presque complètement lisse.

Face externe (fig. 1). On voit seulement la rhinale antérieure avec, sur le rhinencéphale, l'endorhinale. La rhinale antérieure est complètement développée, mais la postérieure, en continuation avec l'antérieure, existe seulement en avant, dans la région de l'angle de coudure. Cette précocité de la rhinale antérieure par rapport à la postérieure qui se développe d'avant en arrière s'observe partout, non seulement chez les Ongulés, mais aussi chez les Carnassiers, et également chez les Primates. Chez les Équidés et chez les Suidés on constate l'extrême précocité de l'endorhinale.

La *face interne* était lisse montrant seulement un début de la fissure hippocampienne (voir stade II).

STADE II

Indice = 75.

Angle des rhinales = 112°.

Face externe (fig. 2). La rhinale postérieure est presque complètement développée. C'est seulement dans sa région toute postérieure qu'elle ne l'est pas encore.

Dans le neopallium, au dessus de la rhinale antérieure et en avant de l'angle des rhinales, est une dépression obscure qui répond manifestement à l'ectosylvia antérieure, l'ectosylvia postérieure étant à peine indiquée. C'est aussi ce que l'on voit chez le porc, mais non chez le cheval où (fait important à noter) le développement de l'ectosylvia commence par celui de l'ectosylvia postérieure.

Face interne (fig. 3). La fissure hippocampienne est très profondément marquée dans les régions retro- et supracommisurale. Elle est interrompue en avant et vers le bord inférieur du cerveau, étant ainsi séparée de la fissura prima de His par une région complètement lisse. Cette disposition est identique à celle que l'on voit chez le porc. Chez le cheval, au contraire, la fissure

[1] Voir R. Anthony et F. Coupin: "Le cerveau de l'ours nouveau né," *Album Soc. Scient Sevcenkianae Ucrainiensium Leopoliensis ad solemn. sua decennalia quinta*, 1873–1923. Leopoli.

hippocampienne se développe en deux segments, l'un supracommisural qui peut même débuter par plusieurs ébauches, l'autre retrocommisural et descendant (indication première du gyrus Andreae Retzii), le premier étant de développement plus précoce que le second.

STADE III

Indice = 73·9.

Angle des rhinales = 112°.

Face externe (figs. 4 et 5). L'ébauche de l'ectosylvia antérieure qui a été signalée dans le stade précédent s'est approfondie. Au dessus d'elle, et un peu en arrière, on distingue une dépression à peine visible, dirigée obliquement d'avant en arrière, c'est l'ébauche de la suprasylvia. Elle vient d'apparaître, car elle n'existe pour encore que sur l'hémisphère droit. La même précocité de la suprasylvia s'observe chez le porc et chez le cheval.

Sur le rhinencéphale, on voit le sillon (α) qui sépare normalement chez l'adulte le gyrus olfactorius lateralis du tractus correspondant.

Face interne. Aucun changement à signaler. Il est à noter que, chez le porc aussi bien que chez le cheval, à l'apparition de la suprasylvia correspond l'individualisation qui ne se manifeste que plus tard chez le bœuf du gyrus dentatus (apparition du sulcus fimbrio-dentatus) dans sa partie toute postérieure.

STADE IV

Indice = 68·9.

Angle des rhinales = 105°.

Face externe (figs. 6 et 7). De l'extrémité supérieure de l'ectosylvia antérieure, se dirigeant en bas et en arrière, part un sillon qui va aboutir derrière l'angle des rhinales et se mettre en contact avec la rhinale postérieure. C'est l'ébauche de l'ectosylvia postérieure beaucoup plus profonde à ses extrémités que dans sa région moyenne.

En avant de l'ectosylvia antérieure, on voit apparaître aussi une dépression courte, mais profonde, à direction à peu près horizontale, c'est l'ébauche de la presylvia. La suprasylvia s'est, d'autre part, développée dans sa région postérieure; elle est maintenant recourbée en forme d'**S** très allongé. Son extrémité antérieure se continue par une dépression peu accentuée qui se continue elle-même par un sillon dirigé parallèlement à la scissure interhémisphérique; ce sillon est tout à fait comparable à celui que nous avons désigné par la lettre β chez le porc; c'est le coronal.

En dedans de la suprasylvia, on voit une ébauche postérieure du latéral et même, à droite, plus en avant, une légère indication de la partie moyenne de ce sillon.

Sur le rhinencéphale, dans la région du lobe piriforme, il y a à noter l'apparition d'un nouveau sillon, le sulcus sagittalis, qui débute par sa partie postérieure.

Face interne (fig. 8). Au dessus de la partie commissurale de la fissure hippocampienne, au niveau du splenium du corps calleux, on voit apparaître

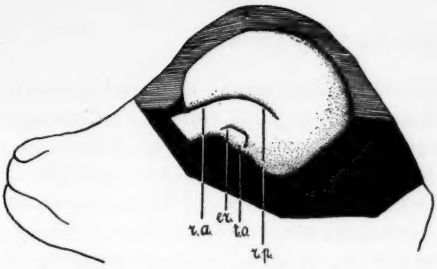

Fig. 1. Stade I (No. 68). Face latérale externe gauche. G.N. ×2.

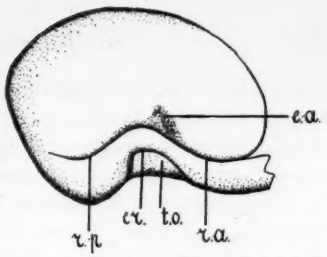

Fig. 2. Stade II (No. 67). Face latérale externe droite. G.N. ×2.

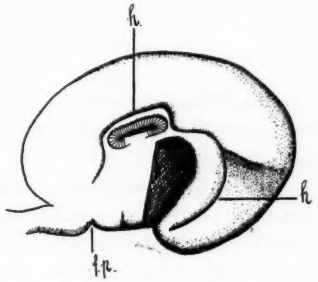

Fig. 3. Stade II (No. 67). Face latérale interne droite. G.N. ×2.

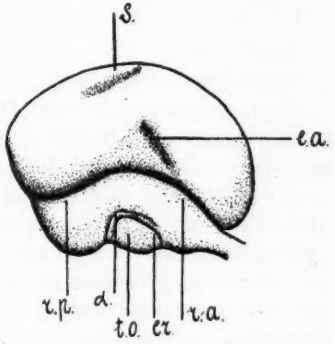

Fig. 4. Stade III (No. 52). Face latérale externe droite. G.N. ×2.

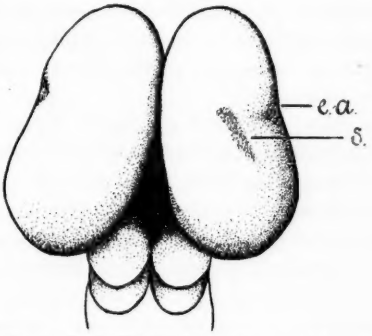

Fig. 5. Stade III (No. 52). Face supérieure. G.N. ×2.

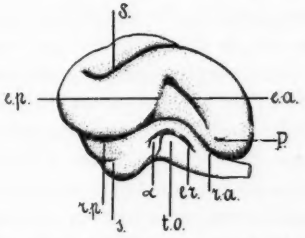

Fig. 6. Stade IV (No. 1). Face latérale externe droite. G.N.

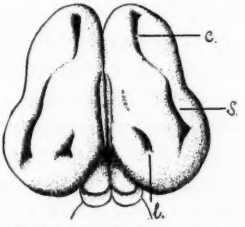

Fig. 7. Stade IV (No. 1). Face supérieure. G.N.

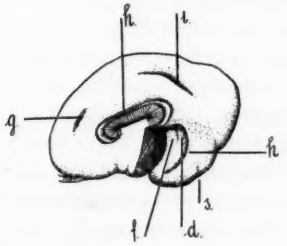

Fig. 8. Stade IV (No. 1). Face latérale interne droite. G.N.

l'intercalaire. D'autre part, une petite dépression marque en avant l'apparition du genualis. Il est à remarquer aussi que le corps calleux s'est allongé et qu'en même temps le gyrus hippocampi s'est retréci dans sa région moyenne, de telle sorte que la fissura hippocampi est maintenant très près du corps calleux.

C'est seulement à ce stade, et par conséquent avec un léger retard par rapport à ce que l'on observe chez le porc que, sur le rhinencéphale, apparaît, par la première indication du sulcus fimbrio-dentatus, le commencement de l'individualisation du gyrus dentatus dans sa partie la plus élevée.

STADE V

Indice = 69·6.

Angle des rhinales = 118°.

Face externe (figs. 9, 10, 11). La suprasylvia, le coronal et le latéral se sont approfondis; le latéral même s'est complété en avant par une partie qui reste encore indépendante de l'ébauche postérieure.

La suprasylvia et le coronal restent indépendants surtout à droite où il n'existe aucune dépression entre eux. De plus, par l'accroissement inégal des parties, le coronal semble maintenant plutôt continuer, comme il est naturel que cela soit, la direction du latéral que celle de la suprasylvia. Rappelons que nous avons noté, chez le cheval, la brièveté et l'apparition plus tardive du coronal.

En avant de la suprasylvia, on voit une petite dépression tout à fait analogue à celle qui existe au même endroit et à un stade comparable chez le porc où nous l'avons désigné par la lettre γ. C'est ici, également semble-t-il, un simple prolongement antérieur de la suprasylvia.

L'ectosylvia postérieure peut à ce stade affecter deux types. Dans un type (No. 33), l'angle qu'elle fait avec l'ectosylvia antérieure n'est pas un angle franc, mais affecte une disposition plutôt quadrangulaire. Dans un autre type (No. 29, fig. 10), une disposition différente s'observe: l'ectosylvia postérieure est constituée de deux parties séparées par un pli de passage, l'une supérieure qui vient en contact avec l'extrémité supérieure de l'ectosylvia antérieure, et se dirige en bas et en arrière, formant avec elle un angle franc, aigu, ouvert en bas, l'autre inférieure qui est une dépression bien marquée disposée dans le prolongement de la partie supérieure, mais nettement séparée non seulement de celle-ci, mais encore de la rhinale postérieure. Cette disposition est celle qui se retrouve le plus habituellement sur le cerveau de l'adulte.

Derrière l'ectosylvia et au dessus de la partie postérieure de la suprasylvia, apparaît un petit sillon (δ) à peu près horozontal. C'est le sillon oblique de M. Holl et de G. Elliot Smith.

La presylvia est plus profonde qu'au stade précédent, mais reste courte et éloignée de la rhinale antérieure.

Sur le rhinencéphale, on voit les mêmes sillons qu'au stade précédent; mais le sulcus sagittalis s'est prolongé en avant.

Face interne (fig. 12). L'intercalaire est bien développé et s'est appro-

fondi; il s'est aussi prolongé vers le pôle occipital et forme ainsi la calcarine dont il faut noter l'apparition tardive qu'on constate d'ailleurs aussi chez le porc et le cheval. Il n'y a pour encore qu'une petite indication du genualis.

La fissura hippocampi se trouve plus rapprochée encore qu'au stade IV du corps calleux par le fait de l'atrophie progressive du gyrus hippocampi. On voit encore nettement le sulcus parolfactorius posterior. Le sulcus fimbriodentatus est développé dans presque toute la moitié supérieure de sa longueur.

STADE VI

Indice = 61·5.

Angle des rhinales = 125°.

Face externe (figs. 13 et 14). Tous les sillons se sont approfondis. La suprasylvia s'est prolongée vers le pôle occipital; elle se continue en avant, comme chez le porc par le vertical qui est indépendant de la suprasylvia à gauche. La presylvia s'est un peu allongée. Sur l'hémisphère gauche, on voit une ébauche d'entolatéral.

Les changements les plus importants sont ceux qui concernent l'ectosylvia. L'ectosylvia antérieure s'est approfondie surtout à ses extrémités, mais n'a guère changé de forme; par contre, l'ectosylvia postérieure diffère profondément de ce quelle était au stade précédent dans le type représenté par le No. 29, en ce que son segment inférieur a pris la forme d'une ligne brisée à angle aigu, ouvert en bas, de telle sorte qu'il semble y avoir deux sillons arqués, l'un au dessus de l'autre, le supérieur étant l'ectosylvia.

Sur le rhinencéphale on voit pour la première fois deux sulci transversi gyri olfactori lateralis.

Face interne (fig. 15). Au dessus de la partie spléniale de la fissure hippocampienne existe un début de calloso-marginal.

L'intercalaire, lié à la calcarine, reste séparé du genualis.

La fissura hippocampi est très rapprochée du corps calleux. Le gyrus dentatus est différencié sur un trajet un peu plus long que dans le stade précédent, mais ne présente pas encore l'aspect godronné qui lui a fait donner son nom.

STADE VII

Indice = 61·9.

Angle des rhinales = 123°.

Face externe (figs. 16 et 17). A ce stade, l'entolatéral existe sur les deux hémisphères.

L'ectosylvia postérieure dont l'aspect si particulier a été signalé au stade précédent n'a guère changé d'aspect.

La branche de prolongement de la suprasylvia (γ) et le sillon oblique de Holl et d'Elliot Smith (δ) se sont allongés considérablement, ainsi que la presylvia. Celle-ci ne vient pas, tout de même, au contact de la rhinale antérieure.

Le vertical est à peine amorcé dans l'exemplaire que nous avons sous les yeux.

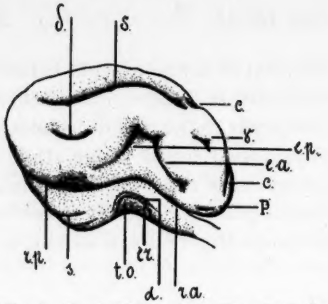

Fig. 9. Stade V (No. 33). Face latérale externe droite. G.N.

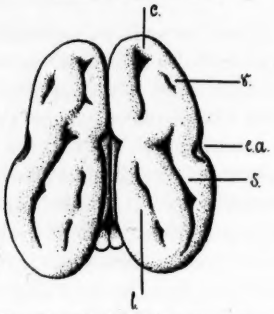

Fig. 11. Stade V (No. 33). Face supérieure. G.N.

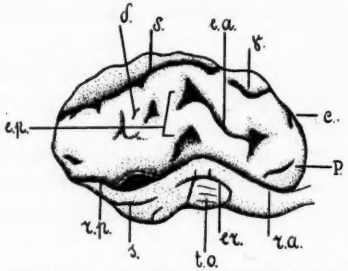

Fig. 13. Stade VI (No. 23). Face latérale externe droite. G.N.

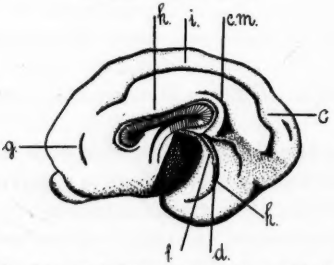

Fig. 15. Stade VI (No. 23). Face latérale interne droite. G.N.

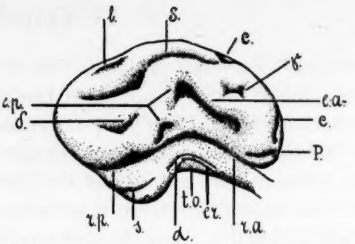

Fig. 10. Stade V (No. 29). Face latérale externe droite. G.N.

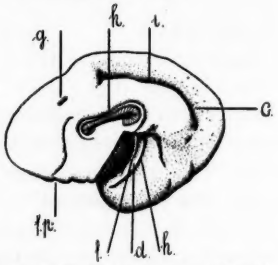

Fig. 12. Stade V (No. 33). Face latérale interne droite. G.N.

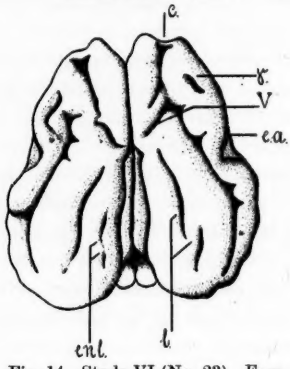

Fig. 14. Stade VI (No. 23). Face supérieure. G.N.

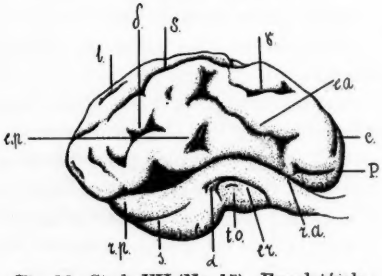

Fig. 16. Stade VII (No. 15). Face latérale externe droite. G.N.

Sur le rhinencéphale, il y a à noter seulement la progression en avant du sulcus sagittalis.

Face interne (fig. 18). La fissure hippocampienne est dans la partie supracommissurale uniquement visible dans ses deux tiers antérieurs, le reste étant invaginé. Le sillon calloso-marginal s'est un peu prolongé vers l'avant, et sa partie toute antérieure est même indiquée au dessus du genou du corps calleux par un petit sillon séparé. L'intercalaire toujours indépendant du genualis présente un sillon perpendiculaire à sa direction à peu près au niveau de la région moyenne du corps calleux. C'est l'amorce du crucial qui, comme nous le verrons, reste très court chez le bœuf.

Sur le rhinencéphale, on voit le sulcus fimbrio-dentatus développé dans toute sa longueur; mais le gyrus dentatus n'a pas encore pris son aspect caractéristique.

STADE VIII

Indice = 64·4.

Angle des rhinales = 128°.

A ce stade, l'aspect de l'adulte est déjà sensiblement réalisé. Tous les sillons fondamentaux sont présents et tous se sont approfondis.

Face externe (figs. 19 et 20). Le seul fait important à signaler est que l'ectolatéral a fait son apparition.

Face interne (fig. 21). Ici, pour la première fois, on voit l'intercalaire lié au genualis.

Au rhinencéphale, le godronnement du gyrus dentatus n'est pas encore visible.

STADE IX

Indice = 66·6.

Angle des rhinales = 126°.

Ce stade ne diffère guère du stade précédent.

Face externe (figs. 22 et 23). Dans quelques cas, on voit la suprasylvia, abstraction faite de son prolongement γ, se réunir par un pli de passage du coronal, de même, le vertical peut manquer (voir fig. 23); la presylvia peut aussi paraître se réunir à l'ectosylvia antérieure.

Face interne (fig. 24). A signaler, dans l'exemplaire examiné, le fait que le genualis n'est pas lié à l'intercalaire.

Le godronnement du gyrus dentatus est ici réalisé.

STADE X

(Voir figs. 25–26 et 27)

Indice = 57·8.

Angle des rhinales = 126°.

Cerveau adulte.

Nous nous bornerons à signaler, sur la face interne, l'accentuation de l'ébauche du crucial.

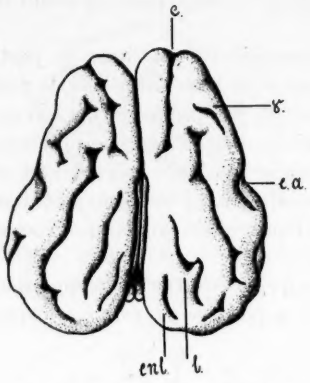

Fig. 17. Stade VII (No. 15). Face supérieure. G.N.

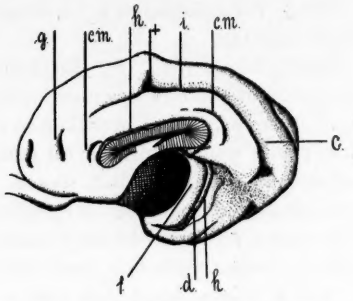

Fig. 18. Stade VII (No. 15). Face latérale interne droite. G.N.

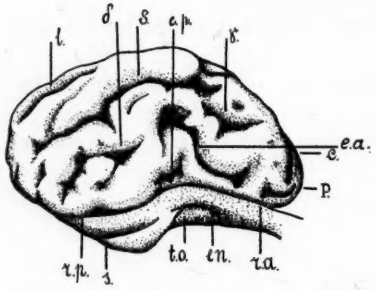

Fig. 19. Stade VIII (No. 3). Face latérale externe droite. G.N.

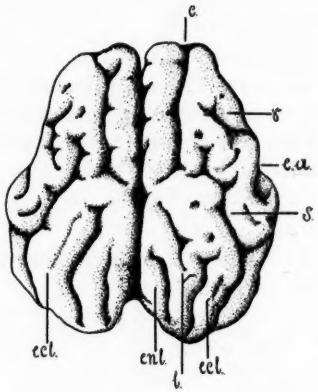

Fig. 20. Stade VIII (No. 3). Face supérieure. G.N.

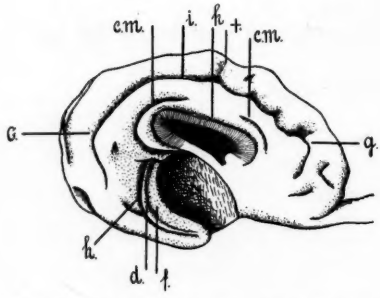

Fig. 21. Stade VIII (No. 3). Face latérale interne gauche. G.N.

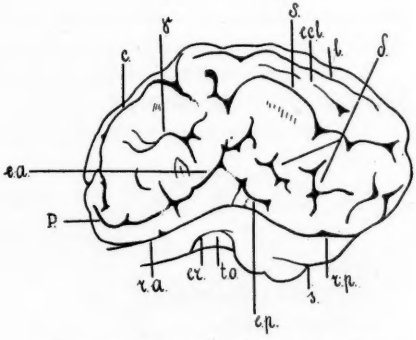

Fig. 22. Stade IX (No. 18). Face latérale externe gauche. G.N.

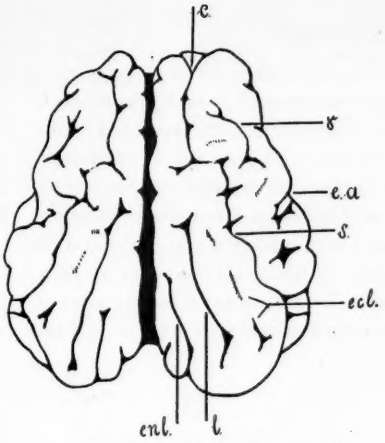

Fig. 23. Stade IX (No. 18). Face supérieure. G.N.

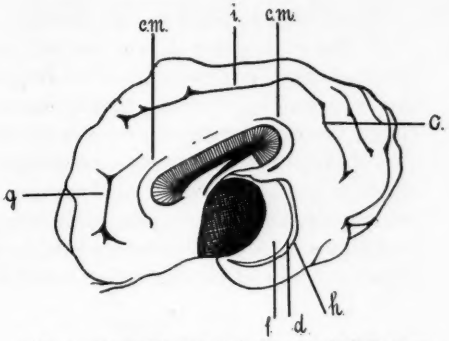

Fig. 24. Stade IX (No. 18). Face latérale interne droite. G.N.

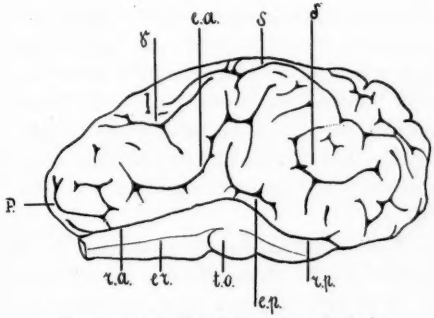

Fig. 25. Stade X (adulte). Face latérale externe gauche. 1/2 de G.N.

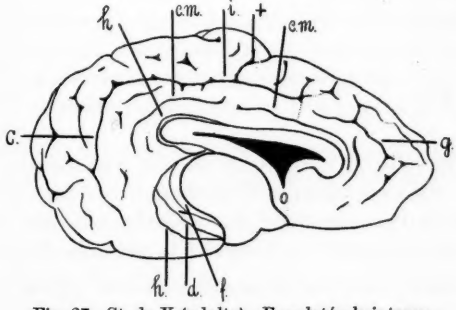

Fig. 27. Stade X (adulte). Face latérale interne gauche. 1/2 de G.N.

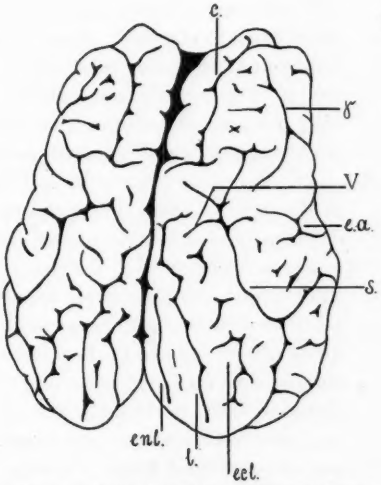

Fig. 26. Stade X (adulte). Face supérieure. 1/2 de G.N.

RÉSUMÉ ET CONCLUSIONS

En résumé, au point de vue cérébral, le bœuf est caractérisé:

1° Par le longueur de son cerveau comparativement à sa hauteur, cette forme allongée, commune à tous les Ongulés, s'accentuant au cours de l'évolution ontogénétique comme chez le cheval et chez le porc. En même temps, l'angle des rhinales devient de plus en plus ouvert, également comme chez le cheval et chez le porc; mais ce processus se développe d'une manière moins régulière que le précédent, car l'angle après s'être ouvert à son maximum se referme légèrement et ceci est encore commun au bœuf, au cheval et au porc. Le tableau et les graphiques ci-joints, les seconds intéressant à la fois le bœuf, le porc et le cheval, indiquent l'accentuation progressive de ces deux caractères.

Stade	Indice	Angle des rhinales	Stade	Indice	Angle des rhinales
I	84·6	—	VI	61·5	125°
II	75	112°	VII	61·9	123°
III	73·9	112°	VIII	64·4	128°
IV	68·9	105°	IX	66·6	126°
V	69·6	118°	X	57·8	126°

De l'allongement du cerveau et de l'ouverture progressive de l'angle des rhinales résulte que la suprasylvia devient presque rectiligne au lieu d'être véritablement arquée comme elle l'est chez les Carnassiers, ce dernier caractère étant considérablement atténué chez les Suidés dont le cerveau est d'ailleurs beaucoup plus près de celui d'un Carnassier, par l'ensemble de sa morphologie, que ne l'est le cerveau des autres Ongulés. Les Suidés s'affirment donc aussi bien par leur neopallium que par la constitution de leurs extrémités et leur dentition des Ongulés de type primitif[1].

2° Par une tendance dès le début à l'operculisation du gyrus arcuatus No. 1 de Leuret, le sillon d'operculisation étant l'ectosylvia. Mais il est curieux de remarquer que cette operculisation ne se poursuit pas. Bien au contraire, le gyrus arcuatus No. 1 s'élargit considérablement, se creusant même d'un sillon arqué qu'on pourrait appeler sulcus arcuatus No. 0 et qui se développe au dépens de la branche postérieure de l'ectosylvia; ceci est différent de ce qu'on observe, d'une part, chez les Suidés où l'operculisation se fait à peu près comme chez les Carnassiers du groupe des Arctoidea, et, d'autre part, chez les Équidés où elle porte surtout sur la région postérieure du gyrus arcuatus No. 1, sa région antérieure restant superficielle et se reliant au territoire périphérique par un important gyrus reuniens.

3° Par l'apparition tardive de la calcarine, fait commun non seulement aux Ongulés, mais aux Carnassiers, qui à cet égard se différencient profondément des Primates chez qui la fosse striée (qui, à la vérité, n'est point la calcarine vraie) apparaît au contraire très tot, sans doute en raison de la présence du

[1] Voir à ce sujet M. Friant: "Contribution à l'étude de la différenciation des dents jugales chez les Mammifères. Essai d'une théorie de la dentition," *Publications du Museum*, No. 1, 1933, Thèse de Doct. ès Sciences.

lobe occipital très développé auquel se lie en même temps l'existence d'un prolongement postérieur du ventricule latéral n'existant pas chez les autres Mammifères.

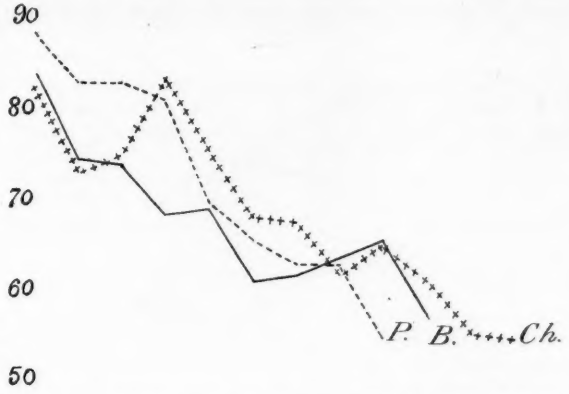

Fig. 28. Graphique destiné à montrer le développement de la forme allongée du télencéphale chez le porc (*P.*), le bœuf (*B.*) et le cheval (*Ch.*).

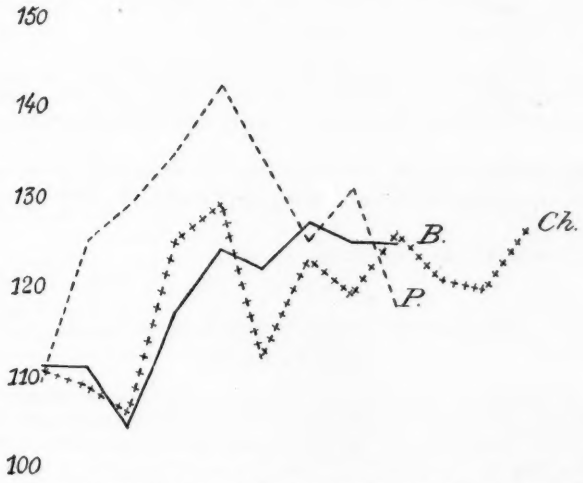

Fig. 29. Graphique destiné à montrer l'ouverture progressive de l'angle des rhinales chez le porc (*P.*), le bœuf (*B.*) et le cheval (*Ch.*).

4° Par l'époque extrêmement tardive à laquelle se développe le crucial et par l'aspect rudimentaire de ce sillon qui reste indépendant du coronal lequel est bien développé. On dit souvent que le crucial n'existe pas chez les Ongulés. C'est donc en partie vrai, au moins en ce qui concerne le bœuf qui nous permet de mieux comprendre les dispositions qu'on observe du crucio-coronal

chez les Suidés et les Équidés. Chez les Suidés, le crucial est très net et allongé se continuant avec le coronal qui va jusqu'à l'extrémité de l'hémisphère. Chez les Équidés, il est bien développé aussi et le coronal très réduit, simplement représenté, semble-t-il, par une petite branche de bifurcation du crucial.

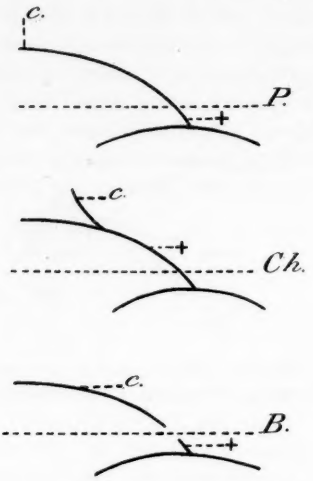

Fig. 30. Schéma destiné à montrer les rapports habituels du crucial (+) et de l'intercalaire chez le porc (*P.*), le cheval (*Ch.*) et le bœuf (*B.*). La ligne pointillée indique la limite des faces externe et interne de l'hémisphère.

Comme chez le bœuf il est de formation tardive, alors qu'au contraire chez le porc, qui se rapproche encore en cela des Carnassiers, il est de formation très précoce.

5° Par le brièveté de la presylvia.

INDICATIONS RELATIVES AUX FIGURES

Signification des lettres

Neopallium: *S.* suprasylvia; *e.a.* ectosylvia antérieure; *e.p.* ectosylvia postérieure; *P.* presylvia; *l.* latéral; *ecl.* ectolatéral; *enl.* entolatéral; *c.* coronal; *V.* vertical; *C.* calcarine; *i.* intercalaire; *g.* genualis; γ, sillon de prolongement de la suprasylvia; δ, oblique de G. Elliot Smith; *cm.* calloso-marginal; +, crucial.

Rhinencéphale: *r.a.* rhinale antérieure; *r.p.* rhinale postérieure; *en.* endorhinale; *t.o.* tuberculum olfactorium; *f.p.* fissura prima de His; *h.* fissura hippocampi; *d.* gyrus dentatus; *f.* fimbria (fornix); *s.* sulcus sagittalis; α, sillon innominé entre le gyrus et le tractus olfactorii laterales.

Les cinq premières figures (stades I, II, III), sont au double de la grandeur naturelle.
Les figures 6 à 24 inclus (stades IV, V, VI, VII, VIII, IX) sont à la grandeur naturelle.
Les figures 25 à 27 inclus (stade X) sont au demi de la grandeur naturelle.

REVIEWS

Early Forerunners of Man. By W. E. Le Gros Clark, D.Sc., F.R.C.S. (London: Baillière, Tindall and Cox.) 1934. Pp. xvi + 295, 89 figs. Price 15*s.* net.

The small community of British anatomists has always been distinguished for the excellence of its work on Man in relation to his Primate ancestors. Everyone knows Sir Arthur Keith's great contributions to our knowledge of the anatomy of the anthropoid apes and of fossil Man. Sir Grafton Elliot Smith, to whom the author dedicates this volume, has especially elucidated the neurological and psychological factors involved in the emergence of Man. Prof. Wood-Jones in a series of books has illuminated the same anatomical problems with scientific imagination and critical insight. Prof. Le Gros Clark, by the publication of the present work, rightfully takes his place amongst these whose reputations have been so justly established.

More than ten years ago Wood-Jones ruffled the surface of British anatomy by proclaiming that not the existing great apes but *Tarsius*, an animal the size of a 2 weeks' old kitten, was the nearest living representative of the ancestors of Man. This provocative statement stimulated the issue of several monographs on Primate anatomy from the department of Sir G. Elliot Smith, and about this time the departure of Le Gros Clark to the far East occurred. The later results were Wood-Jones' *Man's Place among the Mammals*, Gregory's *Man's Place amongst the Anthropoids*, and now Le Gros Clark's *Early Forerunners of Man*.

Le Gros Clark opens his book with a discussion of the methods and principles by which he proposes to test the evidence he assembles. This discussion is excellent, and one appreciates his calm, dignified and good-natured style of writing. He then proceeds to marshal and to weight his evidence system by system—skull, teeth, limbs, brain, special senses, digestive and reproductive systems. The last two chapters deal with the relations of the tree-shrews to the Primates and the evolutionary radiations of the Primates.

Le Gros Clark's special contributions to the problems involved comprise numerous papers and, in addition to a monograph on the tree-shrew, he has published many studies of the cortex of Primates, of the history of the form and differentiation of the thalamus, of the third nerve nucleus, and especially it was he who first perceived that the lateral geniculate body in the Primate inverts in the Lemurs and *Tarsius* and everts in the Anthropoidea—perhaps a character as genetically fundamental as the constitution of the orbit or the relation of internal carotid artery, the typanic bulla and the ectotypanic bone. In addition he made many notable first-hand observations on the arboreal creatures and secured some unique photographs of them while in the East.

Throughout the author sticks to his principles and is not to be caught indulging in logical trimming to suit his convenience. It is necessary to examine not merely the living specimens of Primates but also the whole historical record as far as it is available. Similar trends betoken community of origin. This enables the author to hold together all the usual groups included among the Primates, to add the Tupaiadae and to refuse to cast out the Lemurs. By applying the principle that a special development of some feature must exclude its possessors from ancestory to those which have not this specialisation the author gets back each prosimian group to a small primitive generalised Mammal whose only qualification for starting the Primate stock was its ability to bequeath to its descendants certain trends which it is agreed to regard as the distinctive features of the Primates.

Thus the Lemuriformes, including the Tupaiadae, the Chiromyidae, the Lorisiformes and the Tarsioidea, all must have diverged from the same common ancestors

somewhere about the same time, and no one of these could have directly given origin to any other among them.

It is not, however, unlikely that amongst certain early extinct tarsioids, the Michrochoeridae, the Anthropoids began. If so the common ancestor must have been far more primitive than any known tarsioid. From this anthropoid stem the platyrrhine monkeys must have diverged extremely early as shown by their dentition, the tympanic region, the placentation and the very generalised characters of *Hapale*. Not long after them the catarrhine monkeys separated from the anthropoid stem, and by Oligocene times all three, the platyrrhine monkeys, catarrhine monkeys and the anthropoid apes had separated.

The relatively numerous fossil apes are early derivatives of the stem which gave rise to Man, and some of these fossils (*Australopithecus*) are perhaps richer in human characters than the existing anthropoid apes. If the evidence of foot structure is accepted, then Man must have diverged from the stem which culminated in the living anthropoid apes when the body weight had hardly exceeded that of gibbon. "That Man has been derived from a form which, without imposing any strain on commonly recognised definitions, can be properly called an anthropoid ape is a statement which admits of no doubt."

The statements set out above perhaps are sufficient to indicate the sort of general conclusions to which the author has come. He avoids on the one hand harping, as some do, on the close genetic, if not actually derivative, relationship of Man and the existing great apes. On the other hand Man is not regarded as a surviving member of the giant progeny of the unspecialised tarsioids of the Eocene. Le Gros Clark takes a middle position and indeed after a decade of intense Primate research he who has played a leading part in that period of activity sums up the whole position in terms which will satisfy for they express accurately and with adequate evidence what most have always felt represents the best judgment on the affinities of the Primates.

This book then puts on record the author's and his colleagues' contributions to Primate anatomy and phylogeny. In the light of clearly stated morphological principles it judges all the available anatomical facts and arranges on a genetic plan all the members of the Primate family, thus making an excellent book for the student of these matters. The book however does not stop here. The author bravely faces the great biological issues raised by his studies in comparative anatomy. The Primates are held together by their common trends. Within the whole, larger groups and lesser groups can be distinguished as they add or subtract from the common trends by their own specialisations. Much then in Primate similarity is due to parallelism, while differences come from specialisations which hedge off one group from another or in some cases extend among groups otherwise well separated.

The problem can be illustrated by the behaviour of the lateral geniculate whose morphological value the author discovered. The generalised form of this structure is seen in *Tupaia*. In the Lemurs and in *Tarsius* it becomes inverted while in the catarrhine monkeys it becomes everted. The eversion however is much less in Man and the anthropoid apes than in the monkey. It needs much patience and skill and the examination of a large variety of evidence to come to sound conclusions in the face of such zig-zag specialisation. These trends, which are of course of the nature of orthogenesis, are apparent in the distinctive features of the Primate stock and also in their specialisations, and they constitute for the author as they have done for almost every comparative anatomist the real mystery of evolution. Our author is willing to bow the knee in the temple of the modern geneticist and give these trends a home in the germ plasm. At any rate he feels that they are not to be explained away by any specious application of the principle of natural selection.

The author ends his book with the presentation of a great biological problem while we can congratulate him on having made a very distinguished contribution to British anatomy.

Human Embryology and Morphology. By Sir Arthur Keith, M.D., F.R.S., LL.D., D.Sc., F.R.C.S. (London: Edward Arnold and Co.) 1933. Pp. viii + 558, 535 figs. Price 32*s.* 6*d.* net.

Since the reward of producing a successful text-book for medical students and practitioners is not inconsiderable, there is always a strong inducement to seek this prize. In a country where examining and being examined is ranked as a national industry, and indeed is the solitary example of an industry which flourishes and expands when all else is blighted by the economic blizzard, the temptation to produce a book which by threats and promises seduces the student into believing that herein lies his salvation, is hardly to be resisted.

When a book appears which is unconscious of these interested motives the result is as welcome as it is unusual. Such books for students do occasionally appear. Out of the fullness of the mind and heart such a book may be created and live on because of the sincerity of the author, because of his love for his subject, because it communicates his eagerness, hopefulness and humility. The late Sir William Bayliss created such a book for our sister science when he wrote his *Principles of Physiology.* Sir Arthur Keith has given us a comparable treatise for anatomy.

This book is now in its fifth edition, and for him who desires to seek out the structure of the human body, whence it came, how it grows and differentiates, it is not possible to imagine a more fitting introduction.

At a time when the place of anatomy in the medical curriculum is being seriously questioned, when many ask what can anatomy offer beyond the discipline of the dissecting room, how can it be other than packing the memory with a mass of soon-to-be-forgotten facts—to all such questions and criticisms *Human Embryology and Morphology* is an entirely adequate answer.

It is comprehensive in its approach to the understanding of the structure of the human body, for it gathers its material from the workers of every country and uses all the facts of comparative anatomy, comparative embryology, tissue culture, experimental embryology, transplantation, animal experiment, clinical medicine, pathological processes and anomalies. It is presented in the kindly, lucid, and intimate style of the author and it is rich with the thoughts and ideas of a life devoted to scholarship and investigation.

The book is precious to British anatomists, for it not only elevates their subject and commands respect but also the catholicity and generosity of the author have set their work in the framework to which the many investigators of all countries have added their contributions.

The Radiology of Bones and Joints. By James F. Brailsford, M.D. (London: J. and A. Churchill.) 1934. Pp. xx + 500, 310 figs. Price 30*s.*

According to the preface, the purpose of this book is to set forth concisely an account of the bone changes seen in health and disease, to indicate the significance of the radiographical findings and to present briefly the recent advances already recognised by X-ray specialists, but not yet adequately appreciated by general text-books. It does not attempt to expound the pathology of disease in bone, nor to give a full account of radiographic technique, although many useful hints are included, particularly of recommended positions. No space is taken up by descriptions of common fractures, nor wasted by any unnecessary fullness of style. The result is a book, packed with information and almost encyclopaediac within its set limits, which accurately and amply fulfils its expressed purpose and rigorously avoids irrelevancies.

Normal and pathological appearances are first described in regional fashion. A shorter concluding part contains a general discussion on bone changes in systematic and localised disease. The careful description of normal appearances includes sufficient

reference to ossification times; stress is laid on all deceptive features. The sections on chondro-osteo-dystrophy and on spondylolisthesis deserve special mention. A feature of the work is the wealth of reference to other authorities, documented in a bibliography of nearly a thousand items, but the text is obviously written by one who has himself had wide experience in his subject. Occasional shrewd comments only make one wish that his personality had been less modestly repressed.

The illustrations reach a high standard. The book is printed on heavy glazed paper, so that the figures can all be placed in their appropriate positions in the text. The great majority are photographs; the rest are tracings which include a very useful set of the normal head in various positions.

A general reflection left after reading this book is that the teaching of X-ray anatomy, so much called for nowadays, is not to be lightly undertaken without special knowledge. The anatomist faced with this task will find much useful information in this book (is it too much to hope for a companion volume on the radiology of the other systems of the body?); but it is highly desirable that such teaching should be undertaken by an expert radiologist. The University of Birmingham, in which Dr Brailsford holds the post of Radiological Demonstrator in Living Anatomy, is to be congratulated and its example followed.

Anatomy of the Primates. The Anatomy of the Rhesus Monkey (Macaca mulatta). By Nineteen Authors. Edited by CARL G. HARTMAN and WILLIAM L. STRAUSS, Jr. (London: Baillière, Tindall and Cox.) 1933. Pp. ix + 383, 122 figs., 6 plates. Price 27*s*.

Until now Man is the sole Primate to have text-books devoted to his anatomy; he is now joined by the rhesus monkey, nineteen anatomists having pooled their labours and produced a manual of anatomy that even the highest Primate might be proud of. The older anatomists, in papers devoted to the anatomy of animals allied to Man, were apt to dismiss a structure by the short sentence: "As in Man," as if all men were exactly alike in structure. In this rhesus book each structure is described in its own right and in exact detail. As to the utility of this book there can be no question; every anatomical laboratory will require at least one copy for reference.

From the preface we learn that the project of producing this work was initiated when the American Association of Anatomists met in Charlottesville in 1930, Dr W. E. Sullivan of the University of Wisconsin being the moving spirit. Two editors were appointed, namely, Dr Carl G. Hartman of the Department of Embryology, Carnegie Institution of Washington (in connection with which institution a monkey colony has been established at Baltimore), and Dr William L. Strauss, Jr., of Johns Hopkins University, whose contributions to the anatomy of the Primates is known to many of our readers.

The editors divided the systematic description into 18 sections or chapters, all of them well illustrated, most of the illustrations being by Benjamin Kopel. In Chapter I Dr Gerit S. Miller, Jr., of the National Museum, Washington, discusses the complicated problem of the proper name for the rhesus monkey, deciding in favour of *Macaca mulatta*—which one hopes may serve for some years to come, for the present writer has seen it changed at least three times during the present century. The second chapter is a very excellent one—on the growth and life periods of this macaque, by Dr Adolph H. Schultz of Johns Hopkins University. The skin and its appendages have been done by Dr T. D. Stewart; the hand and foot prints by Dr Harold Cummins. Prof. W. E. Sullivan has taken the long and excellent chapter on the skeleton and joints. The teeth have been described by Dr John A. Marshall, who, like most of the authors concerned, has introduced many new observations into his text. The muscular system has been described by Dr A. B. Howell and Dr Wm. L.

Strauss, Jr., all except the fascial musculature, which is the work of the late Dr Ernst Huhor. Dr Frederick D. Geist has undertaken the anatomy of the nose, mouth and larynx; and Dr P. Lineback the respiratory, digestive and urinary systems. The same author also provides the chapter on the vascular system.

The reproductive system has rightly been entrusted to Prof. G. B. Wislocki of Harvard University. The anatomy of the endocrine glands has been written by two authors, namely, Ruth A. Miller and L. S. Leonard of Columbia University.

The anatomy of the brain has been described, all too briefly, by Dr Marion Hines; the cranial nerves by Dr Kermit Christensen of St Louis University; the spinal nerves by Dr A. B. Howell and Dr Wm. L. Strauss, Jr.; and the autonomic nervous system by Dr Albert Kuntz of St Louis. The anatomy of the ear and eye has been done by Dr T. H. Bast of the University of Wisconsin. Particularly valuable are the lists of references given by the various authors to papers which deal with the anatomy of anthropoid apes and monkeys.

Not the least valuable part of this book is its Appendix, in which Dr Hartman and Prof. George Corner of the University of Rochester give their experiences in the successful management of monkey colonies. Those who wish to rear such a colony will here find the advice needed for housing, heating, ventilating, feeding and handling the commoner kinds.

The Evolution of the Vertebral Column. A Contribution to the Study of Vertebrate Phylogeny. By H. F. Gadow, M.A., Ph.D., F.R.S. Edited by J. F. Gaskell and L. H. H. Green. (Cambridge University Press.) 1933. Pp. xiv+356, 123 figs. Price 25*s.* net.

The material and manuscript for this book had not been entirely put together before the death of the author, and so it was left for others to finish this work. It has been the aim of the editors to complete the book according to the intentions of the author, these being for the most part discernible from his manuscript. Notwithstanding the modest claims of the editors it is clear that they undertook a laborious and difficult task and have carried it to a successful conclusion.

The book is divided into two parts. The first part occupies one-third of the book and is entitled general morphology. Its chapters are concerned with the origin of the axial skeleton, segmentation, composition of standard vertebrae, vertebral processes, articulations, the first three vertebrae, etc.

The second part is devoted to systemic morphology and naturally deals at considerable length with the Reptiles and Mammals.

For more than forty years Prof. Gadow concerned himself with the problems that have been indicated in this inadequate summary of the contents of his book. His active interest in the field of morphology grew more ardent with time, and anatomists are grateful to the editors for their unselfish labours. This book makes a permanent record of the investigations and reflections on the morphological problems of the vertebrate phylum which occupied the fine intellect of Prof. Gadow throughout his active life.

John Keats's Anatomical and Physiological Note Book. Printed from the Holograph in the Keats Museum, Hampstead. Edited by Maurice Buxton Forman. (Humphrey Milford: Oxford University Press.) 1934. Pp. xi+68. Price 12*s.* 6*d.* net.

This book contains notes on a series of twelve lectures on physiology and notes on anatomy made by John Keats while a medical student at Guy's Hospital. The physiology notes appear to have been taken down directly from the lectures; while

the notes on anatomy are very neatly written and arranged. The editor has endeavoured to preserve the character of the note-book and the arrangement of the original as far as reasonably possible.

It is of course a matter of great interest to have these notes the originals of which are in the Hampstead Library, and we are grateful to the Editor and the Library Authorities. These notes present abundant evidence that Keats was working earnestly as a student, and in recording the statements and opinions of his teachers he has left an interesting, if brief, record of what was taught him and how he received it. Thus he records that Mr C. (Sir Astley Cooper) believes that the nerves support the organisation of the body but do not directly afford it nourishment.

Three hundred and fifty copies of this book have been printed.

Neuro-Anatomy. A Guide for the Study of the Form and Internal Structure of the Brain and Spinal Cord. By J. H. GLOBUS, B.S., M.D. 6th edition. Foreword by H. D. SENIOR. (London: Baillière, Tindall and Cox.) 1934. Pp. xvi + 240, 36 figs., 52 plates. Price 16*s.* net.

This practical manual sets out the programme of practical classes for studying the central nervous system which, judging from the success of the book, must be used by numerous schools in America.

The work is divided into twenty-three assignments each of which is expected to occupy the student about three hours. These assignments start, of course, with the external anatomy and pass to the study of the internal anatomy by horizontal and serial transverse slices of the brain and cord. The anatomical study is completed by Weigert sections from appropriate levels.

Explanatory and descriptive text, concise but adequate, is provided. Further outline drawings on detachable sheets to be filled in and labelled by the student are available thus saving much time, a commendable object which the author emphasises. Figures already labelled and others ready to be labelled are also given as well as serial sections so superimposed that the origin and destination of the more important pathways can be added in colour.

Each assignment begins by giving the necessary dissecting instructions for displaying the list of structures to be studied; the numbers of the outline drawings to be filled in and sketches to be labelled; and two or three titles to guide collateral reading and serve as subjects for essays. Then follows the descriptive and explanatory text.

It is all most admirable.

Human Sex Anatomy. By ROBERT LATON DICKINSON, M.D., F.A.C.S. A Topographical Hand Atlas. Medical aspects of Human Fertility. Series issued by the National Committee and Maternal Health, Inc. (London: Baillière, Tindall and Cox.) 1933. Pp. xiv + 145, 191 figs. Price 45*s.* net.

The author has attempted to establish an accurate knowledge of the living anatomy of reproductive organs in the male and female. The implications of these anatomical data on sex life, fertility and the like are discussed.

The book is illustrated by 173 outline drawings, mostly life-size, of the subject-matter. There are 119 pages of text, with bibliography and index.

The book is dedicated to Havelock Ellis.

Life in the Making: The Story of Human Procreation. By ALLAN FRANK GUTTMACHER. (Jarrolds, Ltd.) 1934. Pp. 288, 8 figs. Price 10*s.* 6*d.* net.

The issue of books about reproduction, generation, procreation and the like has naturally always been going on. The success which has attended recent investigation of these problems has, naturally, considerably increased their output.

The present book is a very good one, and against the background of superstition, priestcraft and error presents the newly gained knowledge with clarity and precision.

The first part presents the prescientific ideas on how life begins and ends with the discovery of sperm and egg by the use of the scientific method.

The second part presents in broad outline the reproductive phenomena from amoeba to man, and includes chapters on the relationship of the gonads to sex differentiation, on sex determination, sterility, and fertility and twinning.

The author, who is an associate in obstetrics at Johns Hopkins University, writes of course with real knowledge of his subject and has enlivened his narrative by the incorporation of examples of popular credulity from the gossip, folk-lore, and fables of reproduction.

Principles of full Denture Prosthesis. By E. WILFRED FISH, M.D., L.D.S. (London: John Bale, Sons and Danielsson, Ltd.) 1933. Pp. ix+100, 31 figs. Price 10*s.* 6*d.* net.

This book contains a very interesting presentation of the principles which govern the stability of complete dentures. These are discussed in relation to the occlusal surface, to the impression surface and finally in regard to the polished surface. This last surface is that which comes into relation with the muscles of the face, and the author presents a most interesting account of the muscular pivot known as the modiolus or as Knoten to German authors. Here eight facial muscles meet in a nodal point and each makes its contribution in determining the final position of the modiolus—and affects the stability of a denture of the lower jaw.

The very interesting exposition of how a denture should be constructed in order to take advantage of these muscles of the face such as the orbicularis, the buccinator, the caninus, zygomaticus, the triangularis, etc., leads one to make the comment that those anatomists who have to teach and examine dental students should perhaps remember that these facial muscles are of considerable importance in the practice of successful dentistry.

Krebs im Lichte Biologischer und Vergleichend Anatomischer Forschung. Von Med. Dr Jos. LARTSCHNEIDER, Linz a. d. Donau. I. Band: *Ectoderm-krebs.* (Leipzig und Wein: Franz Deuticke.) 1934. Pp. 192, 48 figs. M. 10.

This book, the first volume of its series, approaches the problem of skin cancer not from the point of view of cellular proliferation nor from the point of view of humoral pathology, but rather in terms of the normal behaviour, organisation and productive manifestations of skin.

These latter are only to be discovered through the comparative anatomy of the integument, its anatomical reactions to such conditions as life in the water or nutritive deprivation, and by a study of the various kinds of chemical scaffolding, the horns, hoofs, mantles, etc., which come from it.

The external surface of the higher Vertebrates is covered by a horny mantle. It is beneath this keratotic layer that a parakeratotic layer lies which is the external layer of Amphibia, etc. The presence of a keratotic layer renders the skin immune to cancer;

its absence favours the growth of cancer. Since this parakeratotic layer, favourable to the production of cancer, forms the external covering of the Amphibia throughout the whole of their post-larval lives, cancer should be common in the skin of the frog. The author maintains this is so, and furthermore, the cancer in these cold-blooded animals, being of necessity uncomplicated by inflammatory reactions, can be studied under the most favourable conditions. The author's views depend much on the observations made on the skin of frogs.

A Short History of Physiology. By K. J. FRANKLIN, D.M. (London: John Bale, Sons and Danielsson, Ltd.) 1933. Pp. iv + 122. Price 3*s.* 6*d.* net.

This brief but extremely interesting history of physiology was written by Dr Franklin for his students. It is certain that students outside his own school would also be instructed and entertained by this book.

Within the limits imposed by the size of the book sufficient space is given to the ancient world and to the period of the Renaissance. More space is properly given to the recent times during which physiology has been so prolific, and it is indeed a matter not only of interest but sometimes of need to have an accurate compendium of names, dates and places associated with particular modern discoveries. The professional historian usually omits such information, and it needs one like the present author, historian and physiologist in one, to apportion and allocate the more recent achievements.

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